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THE SYSTEMATIC POSITION OF *BROWNEICHTHYS ORNATUS* WOODWARD (PISCES, ACTINOPTERGII)

BY

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[Communicated by Professor G. E. H. Foxon. F. Z. S.—Accepted 10th December 1957]

(With 1 plate and 2 figures in the text)

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INTRODUCTION

The genus *Browneichthys* contains a single species *B. ornatus*. Both genus and species were based by Woodward (1889) on a single incomplete specimen from the Lower Lias of Barrow-on-Soar, Leicestershire. When studying the family Saurichthyidae, to which this species had been provisionally referred (Woodward, 1895), through the kindness of the Authorities of the City of Leicester Museum I had the opportunity of examining the holotype and came to the conclusion that the reference of *Browneichthys ornatus* to the Saurichthyidae cannot be maintained in the light of our present knowledge of that family. Its systematic position is reconsidered here. In addition, as no illustrations of the holotype have ever been published, the opportunity has been taken to prepare both photographs and drawings of it. It has not been possible to add much to the original description but I have redescribed the specimen so that the illustrations may be understood, and my comments on its systematic position be more easily followed.

DESCRIPTION OF THE HOLOTYPE

The only recorded material of this species is the holotype in the City of Leicester Museum. It was originally described by Woodward (1889) and a photograph of the whole specimen is shown in Pl. 1, fig. 1.

The animal was certainly fairly small, the portion present in the specimen being about 6 cm. long, but it is impossible to estimate the total length of the animal when intact. The skull is badly crushed and apart from the orbit very little can be identified with certainty ; a few parts have been tentatively labelled in Fig. 1. Some distance from the remainder of the head lies a large flattened bone, not described by Woodward, that from its shape and size appears to be part of the opercular series, possibly the opercular bone itself.

No teeth are visible. Most of the bones of the skull are ornamented on their external surfaces with tubercles of ganoine

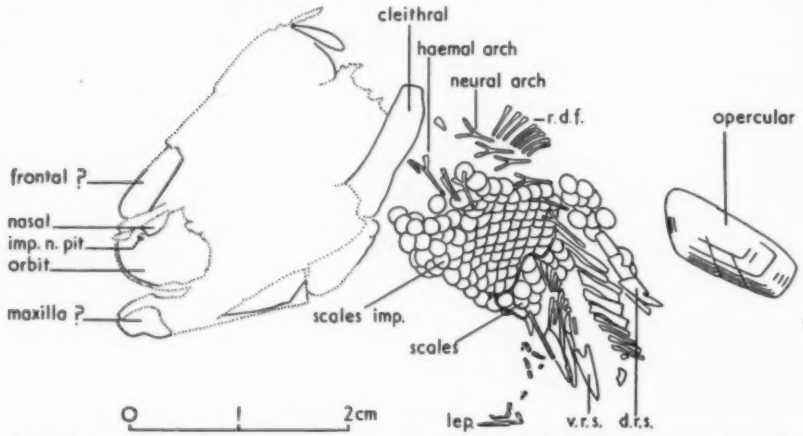

Fig. 1.—*Browneichthys ornatus*. Holotype. d.r.s., dorsal ridge scale ; imp.n.pit, impression of nasal pit ; lep., broken lepidotrichia ; r.d.f., endoskeleton of dorsal fin ; scales, scales of left side ; scales imp., impression of scales of right side ; v.r.s., ventral ridge scale.

The vertebral column is represented by ossified neural and haemal arches separated by a wide space presumably occupied in life by a persistent notochord. In the part preserved each neural and haemal arch bears a prominent median spine. There is no sign of ossified ribs. No fins are preserved, but dorsally there is a series of eight small bones which are probably the endoskeletal supports of the dorsal fin (Fig. 1, r.d.f.).

The body bears small, rounded, deeply overlapping scales with well marked concentric growth lines, and ganoine tubercles on their exposed portions (Fig. 2, Pl. 1, fig. 2). In addition there are a number of long, triangular ridge scales which formed mid-dorsal and mid-ventral lines the extent of which is

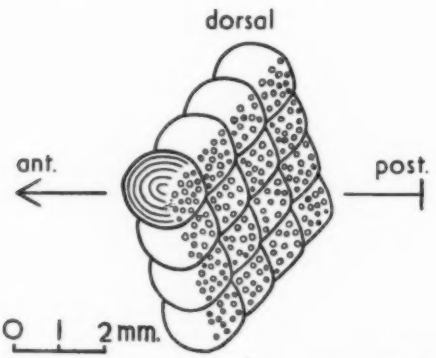

Fig. 2.—*Browneichthys ornatus*. Reconstruction of flank scales.

not known (Fig. 1, d.r.s., v.r.s.). Although, except for the ridge scales, the more posterior part of the specimen lacks scales, there is no reason to suppose that this is other than an accident of preservation and it seems most probable that the whole body behind the head was so covered.

In the posterior part of the specimen the neural and haemal arches are markedly stouter than in the more anterior portion and it is possible that this, together with the presence in this region of well developed ridge scales, indicates that the caudal fin began near this point.

DISCUSSION

In the original description Woodward wrote that " So far as can be determined, the new Barrow fossil thus most nearly approaches the early Mesozoic Ganoids, *Belonorhynchus* and *Saurichthys*. From these, however, and from other types with a persistent notochord, it is generically distinguished by the squamation ". In a later publication (1895) he provisionally includes *Browneichthys ornatus* in the Belonorhynchidae = Saurichthyidae, a view with which later authors have agreed (Stensio, 1925 ; Berg, 1940).

The specimen certainly resembles the saurichthyids in having a persistent notochord, in the presence of ridge scales which may have formed continuous mid-dorsal and mid-ventral series, and in the presence of ganoine tubercles on the dermal bones of the head. But these features are inconclusive in themselves as they are shared by many families of fish in addition to this one. The only evidence in support of the view that this species is a member of the Saurichthyidae is the supposed elongation referred to in the original description in the following way, " The fish must have been originally elongated in form ; and the hinder portion of the head, preserved as far forward as the front margin of the orbit suggests the attentuation of the snout ". As can be seen from Fig. 1 and Pl. 1, fig. 1, the basis for Woodward's conclusion seems slight, the skull for example might quite as easily have ended in a rounded snout just anterior to the orbit. There is certainly no sign of the extreme elongation characteristic of the saurichthyids.

On the other hand there are a number of reasons why *Browneichthys ornatus* should not be included in the Saurichthyidae. If the head is left out of the argument and the body alone considered, two possibilities have to be borne in mind. Firstly, and as I consider most likely, the major part of the trunk is included in the specimen which thus shows no sign of elongation. Secondly, if only the anterior portion of an elongated trunk is preserved, the dorsal fin is seen to be situated in a very forward position as compared with the position it occupies in all the other members of the family in which the trunk region is known, for it is characteristic of the Saurichthyidae that the dorsal and anal fins are borne far back on the body.

Again, considering the squamation, it is found that in the majority of the Saurichthyidae the scales are either reduced to four, three, or two longitudinal rows or are absent altogether. The few species in which a complete scaly covering appears to have been present are of Lower Triassic age and are amongst the earliest known members of the family. In these the scales are roughly in the shape of parallelograms longest in the dorso-ventral direction,

and they show differentiation of the mid-dorsal, mid-ventral and lateral line rows which alone persist in later forms. The distribution of the scales on the body and their shape in *Browneichthys ornatus*, which I have just described, is so unlike the saurichthyid condition, especially when compared with the contemporaneous genera *Acidorhynchus* and *Gymnosaurichthys*, that it is rather difficult to agree with Woodward that the difference is one of generic value only.

What then is the true systematic position of this species? The characters available to decide this are as follows :

1. The endoskeleton of the dorsal fin is not concentrated, and apparently consisted of one row of radials.

2. The vertebral column was composed of a persistent notochord with ossified neural and haemal arches.

3. The body was covered with moderately thin, rounded or cycloidal scales ornamented externally with ganoine tubercles.

4. The animal was of small size and, if my interpretation is correct, more or less fusiform in shape, being neither elongated nor noticeably deepened in a dorso-ventral direction.

5. The species is of Lower Liassic age.

The unconcentrated nature of the endoskeleton of the dorsal fin may be called an actinopterygian character. The construction of the vertebral column indicates that the fish is a fairly primitive actinopterygian and almost certainly belongs either to the order Palaeoniscoidea or the order Sub-Holostei using these terms in the same sense as Brough (1936, 1939). Unfortunately it is impossible to proceed further than this with certainty owing to the incomplete nature of the specimen. However, there is one family, members of which show all the above mentioned characters. This is the Coccolepidae Berg, 1940 (order Paleoniscoidea). There appears to be no reason why *Browneichthys ornatus* should not be included in this family and this step is therefore proposed, though of course one cannot be certain that the discovery of more information concerning this species will not necessitate a further reassessment of its systematic position.

SUMMARY

The unique holotype of *Browneichthys ornatus* Woodward has been re-examined. Illustrations of the specimen are published for the first time, and, although it has not been possible to add considerably to the text of the original account, a short redescription is included. The systematic position of *Browneichthys ornatus* is discussed. It is concluded that this species should not be retained in the family Saurichthyidae and its transfer to the family Coccolepidae is proposed.

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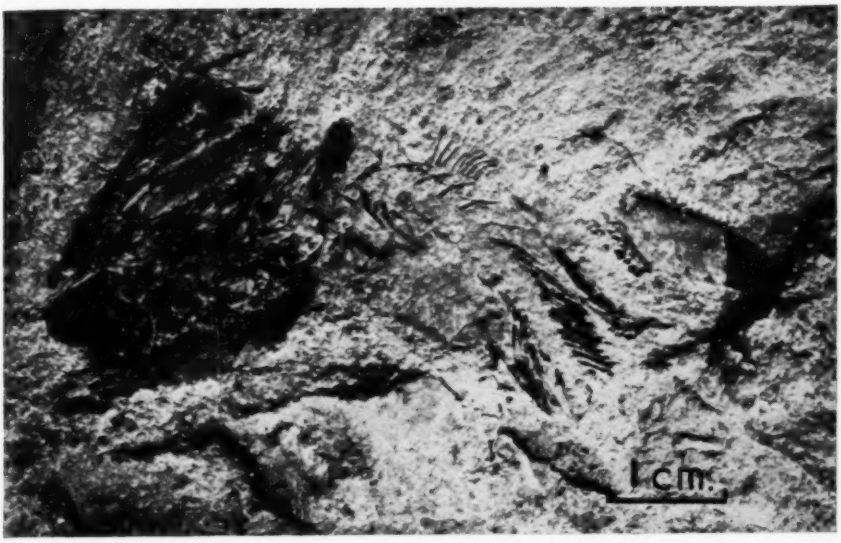

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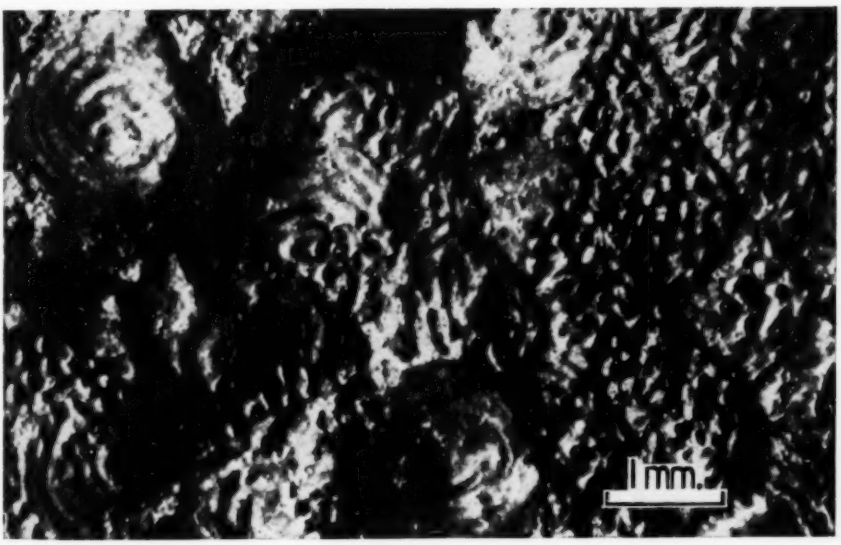

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Browneichthys ornatus

1. Holotype

2. Impression of flank scales

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POPULATION CHARACTERISTICS OF HOUSE MICE LIVING IN ENGLISH CORN RICKS: DENSITY RELATIONSHIPS

BY

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[Communicated by H. N. Southern—Accepted 10th December 1957]

(With 2 figures in the text)

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INTRODUCTION

This paper describes certain population attributes of house mice (*Mus musculus*) living in English corn ricks. A total of 4212 house mice of all ages was collected from forty ricks at the time of threshing in the winter, spring and early summer of 1954–55. The ricks were in the vicinity of Oxford, in the counties of Oxfordshire and Berkshire.

Rick populations of rats and mice were studied in considerable detail throughout the 1940's by members of the Bureau of Animal Population, Department of Zoological Field Studies, Oxford University (Venables & Leslie, 1942 ; Southern & Laurie, 1946 ; Laurie, 1946 ; Chitty & Southern, 1954). Much information is available, therefore, on the degree of rodent infestation in ricks, the growth of rick populations, the seasonal reproductive rates of these populations, etc. It is well known, for example, that many ricks become infested with rats and mice soon after their construction in August and September of each year. The resulting populations frequently reveal rapid growth, and may increase at rates approaching those of a theoretical Malthusian population subject to certain optimal conditions (Leslie, Venables & Venables, 1952). Such populations have attained levels of 2000 mice and densities of fifteen weaned mice per cubic metre within eight months after rick construction. It has been established that reproductive rates of rick

populations show no marked winter decline characteristic of many populations of house mice (Laurie, 1946). Marking studies have indicated that rats enter and leave a rick freely, but that mice, upon entering a rick, stay within its confines until threshing (Southern & Laurie, 1946).

The particular approach of this paper is to examine the demographic traits of rick populations in relation to density of the population. Many recent studies of confined or semi-natural house mouse populations have demonstrated relationships between crowding and reproductive performance (Brown, 1953 ; Strecker & Emlen, 1953 ; Southwick, 1955, 1955 a ; Calhoun, 1956). These studies have generally emphasized the reductions or cessations of population increase which have occurred in crowded populations ; reductions occurring via severe impairments of fecundity or fertility, marked increases in mortality rates, or combinations thereof.

Rick populations provide excellent opportunities for the study of density phenomena in natural habitats. Rick populations are perhaps unique in presenting the following combination of factors favourable for study : (1) the possibility of obtaining large, unbiased samples of a mammalian population, (2) the relative isolation of the population, (3) the favourable habitat with essentially unlimited food supplies, (4) the rapid reproductive rates of the populations resulting in high densities within a short span of time, and (5) the known age of the population.

Rick populations also present many practical difficulties, prominent among which is the impossibility of obtaining an accurate continuous record of a population. One must be content with an instantaneous cross-section of a population, and a sampling method that destroys the population. Hence, all demographic comparisons between populations are limited to the age and fertility structures at the moment of collection.

In the main part of this paper, rick populations are grouped into four major density classes, and the resulting averages of population attributes are compared.

METHODS

The accurate collection of a rick population at the time of threshing depended upon the construction of a fine-mesh string or wire netting around the rick, about five feet from its base. As sheaves were lifted from the rick by the threshing men, mice scurried out and they could be caught with gloved hands and killed immediately. If many came out simultaneously, most ran back into the rick, but those attempting to escape were usually retained by the net.

Some mice managed to get through the net, others were thrown into the threshing machine with the sheaves. By counting the escapes, and by examining the " cavings " trays of the threshing machine for corpses, it was possible to obtain a reasonably accurate estimate of the total population. All available evidence suggested that a 75 per cent unbiased sample could usually be obtained.

Not every rick was suitable for collection purposes. Some ricks were constructed adjacent to hay stacks, stone walls or buildings and an encircling

net could not be constructed. Other ricks were threshed over a period of several days. Still other ricks had been poisoned directly. For the data in this paper, only unpoisoned wheat and oat ricks, threshed in one or two days, and permitting good collecting conditions, were utilized. Ricks with these qualities constituted less than one-half of all the threshings attended during the study period.

After collection, the mice were placed in refrigeration until they could be examined. At autopsy the mice were sexed, weighed, measured, examined for breeding condition internally, and occasionally the adrenal glands and spleen were removed for weighing. Specific details of autopsies will be given in the appropriate sections.

RESULTS

1. Population size : Influence of rick composition and location.

Rick populations attained widely variable levels. For example, ricks of eight to ten months of age contained populations varying from under 200 mice to almost 2000 mice per 100 cubic metres (Fig. 1). This is not surprising, for ricks obviously vary in their size, in their potential infestation sources, in their quality of grain, in the presence or absence of weasels (*Mustela nivalis*) and stoats (*M. erminea*), in their time of construction, etc. Yet this variability is at the same time interesting because ricks do represent a habitat

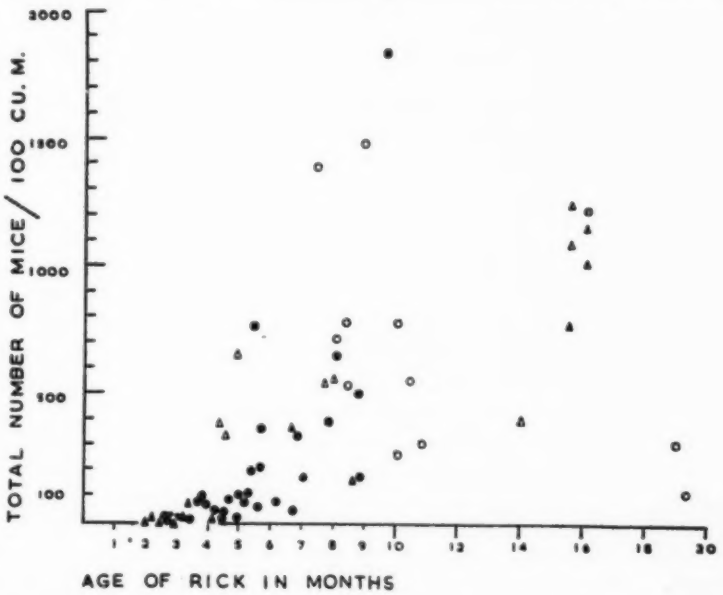

Fig. 1.—Total numbers of mice attained in rick populations of various ages. Circles represent wheat ricks ; triangles represent oat ricks. Solid figures represent ricks threshed in 1954–55 ; open figures represent ricks threshed in 1942–45. The 1942–45 data were kindly furnished by H. N. Southern.

of rather remarkable uniformity in many basic characteristics. That is, practically all ricks provide a dry, warm habitat with cover of exceptionally high quality and abundant supplies of high protein food.

A complete analysis of the variability in population size of rick mice would be impossible on the basis of forty populations. Two obvious variables which can be subjected to preliminary evaluation, however, are the composition of the rick, wheat or oats ; and the location of the rick, field border or farm yard. I shall arbitrarily define a yard rick as a rick within 30 metres of farm buildings (usually within 10 metres), and a field rick as one more than 30 metres from farm buildings (usually at least 100 metres).

Table I shows the bimonthly averages of total population size in four classes of ricks : yard wheat, yard oats, field wheat, field oats. The table clearly shows that wheat ricks have larger populations than oats ricks, and also that yard ricks have considerably larger populations than field ricks.

TABLE I

Average total population size per 100 cubic metres in four basic rick types (numbers of populations in parentheses).

	Yard Ricks		Field Ricks	
Season	Wheat	Oats	Wheat	Oats
Nov.–Dec., 1954	47·5 (3)	46·4 (2)	9·2 (2)	12·8 (5)
Jan.–Feb., 1955	137·3 (6)	81·1 (1)	44·5 (3)	5·2 (1)
Mar.–Apr., 1955	309·1 (3)		65·4 (3)	
May–June, 1955	1131·8 (3)	281·2 (2)	375·8 (3)	

The first conclusion, that wheat ricks contain more mice than comparably situated oats ricks, was reached by Southern & Laurie in 1946. This difference is probably not associated with the food quality of the two grains (wheat and oats are foods of similar nutrient value according to Brody, 1945), but with the physical characteristics of the ricks. Wheat possesses a stronger straw than oats, and this results in a rick with more space between sheaves. Wheat ricks would be easier for mice to penetrate and colonize than oat ricks.

The latter conclusion, that yard ricks have larger populations than field ricks, was not shown to such a marked extent in former data. Previous work has demonstrated that the house mouse is a common species in fields and hedgerows throughout the Oxford region, (Southern & Laurie, 1946). Hence, most ricks in the area studied were probably susceptible to infestation. Apparently, however, yard ricks are more readily infested by large numbers of mice than are field ricks, despite intensive poisoning in and around farm buildings (poisoning campaigns are, of course, directed primarily toward rat populations). The construction of field ricks, rather than yard ricks, could greatly diminish mouse damage according to these data.

Grouping the ricks according to location and grain type reduced, but certainly did not eliminate, the variability in population size. For example, in three yard wheat ricks eight to ten months of age, population size still varied from 500 to 1600 mice. This variability might be attributable to differences in the infestation sources, the rates of reproduction, the stages of

population growth, the presence or absence of predators, etc. The infestation rate is quite probably of greatest importance in producing this variability in population size.

II. Relationships of demographic traits to density

Sizes of ricks in this study varied from 40 cubic metres to 150 cubic metres. By dividing the number of postweaned mice present in a rick by the cubic metre capacity of the rick, figures varying from 0·01 to 16·18 were obtained. These figures represent a crude index to population density. They do not, of course, represent actual or effective population density. It may be assumed that the actual population density, or actual degree of social contact, is some unknown figure larger than this density index.

The data of this section are grouped into four density classes as shown in Table 2. These density classes are arbitrarily defined as follows : low density, less than 0·50 weaned mice per cubic metre ; medium density, 0·50–2·00 weaned mice per cubic metre ; high density, 2·00–6·00 weaned mice per cubic metre ; very high density, over 6·00 weaned mice per cubic metre. Actually the groupings were somewhat more distinct than the above indicates. The adjectives " low ", " medium ", " high ", and " very high " were based upon subjective judgment after being familiar with more than eighty individual threshings.

TABLE 2

Sample sizes and groupings (sample ranges in parentheses).

	Low Density	Medium Density	High Density	Very High Density	Totals or Averages
Number of populations studied	21	11	7	1	40
Average population size : estimated total number of mice	34 (5–102)	118 (60–208)	350 (264–558)	1600	
Average population density : number of weaned mice per cubic metre	0·23 (0·01–0·48)	1·12 (0·50–1·94)	3·50 (2·69–5·64)	16·18	1·45
Average age of population	4 months (2–6·5)	6 months (4–8·5)	7·5 months (5–9)	8·5 months	
Number of mice examined	616	1101	1983	512	4212

In making " density " comparisons of this type, it is difficult and sometimes impossible to distinguish between three general types of effects : (1) density effects, (2) complex population-maturation effects involving altered population structure and social behaviour, and (3) seasonal effects. No claim is made in this paper to separate the first two types of effects. In fact, the paper is primarily a comparison of young, low density populations with mature, high density populations. The observed differences between the populations may be correlated with density, but they cannot be considered strictly density effects.

On most topics the data permit an independent assessment of seasonal effects. Generally, it can be stated that little or no seasonal effect *per se* on population behaviour could be found. For example, no obvious seasonal influence on the fertility of the populations appeared in these data ; pregnancy rates remained high throughout all seasons studied.

With these reservations in mind, the following population comparisons are offered.

A. Basic weight structures

Table 3 groups the mice of the various density classes into three weight groups : 7·5 grams and less, 7·6 to 12·5 grams, and over 12·5 grams. I have chosen these weight groups because I feel that they correspond approximately to three prominent stages in the life of an individual ; namely, the preweaned stages, the postweaned but immature stage, and the mature stage.

The weight distribution of the highest density class suggests maturation of the populations, for it revealed a significantly low percentage of mice under 7·5 grams and a significantly high percentage of mice over 12·5 grams. It is interesting that the highest percentage of individuals under 12·5 grams occurred in the medium density class. This suggests Allee's principle of optimal population size, but the same principle is not shown in the fertility data (sections C and D below).

TABLE 3

Weight distribution. Percentages of samples in each of three major weight groups (actual numbers of individuals in parentheses).

Weight Class	Low Density	Medium Density	High Density	Very High Density	Totals
Less than 7·5 gms.	38·6 (238)	41·1 (452)	36·9 (732)	21·5 (110)	36·4 (1532)
7·6–12·5 gms.	17·4 (107)	17·6 (194)	15·0 (298)	25·4 (130)	17·3 (729)
over 12·5 gms.	44·4 (271)	41·3 (455)	48·1 (953)	53·1 (272)	46·3 (1951)
Percentages of individuals under 12·5 gms. to total individuals	56·2	58·7	52·5	46·9	53·7
Chi-Squares[1]	1·2798	11·0498**	2·4846	12·1688**	

[1] Chi-Squares are calculated on the ratios of individuals under 12·5 gms. to the total individuals in each density class ; they are based upon the hypothesis of homogeniety. One asterisk indicates significant deviation from the hypothesis within the 5 per cent level of confidence ; two asterisks indicate significant deviation within the 1 per cent level of confidence.

Perhaps the most striking fact in Table 3 is the similarity of pattern in weight distribution throughout the density classes.

B. Sex ratios

The percentages of males in three different weight classes are shown in Table 4. No prominent trend in sex ratios is apparent throughout the range of density classes, except a slight depression of male sex ratio in the very high density class.

TABLE 4

Sex ratios. Percentages of males in each of three major weight groups.

Weight Class	Low Density	Medium Density	High Density	Very High Density	Totals	Chi-Squares[1]
less than 7·5 gms.	49·7	54·3	49·3	58·3	51·2	0·3694
7·6–12·5 gms.	41·1	44·8	48·3	49·2	46·5	3·5679
over 12·5 gms.	46·9	44·4	45·1	38·2	44·2	23·6417**
Totals	46·5	46·2	46·4	43·6	46·0	
Chi-Squares[2]	0·0487	0·0204	0·1688	1·0824		

[1] Chi-Squares calculated on totals ; based on hypothesis of 50 per cent sex ratio. Two asterisks indicate significant deviation within the 1 per cent level.

[2] Chi-Squares calculated on totals ; based on hypothesis of homogeniety.

A significant trend in sex ratios does occur, however, throughout the weight classes. The sex ratios of mice under 12·5 grams are not significantly different from a 50 per cent ratio, but over 12·5 grams a significant depression of male sex ratio occurs. This shift presumably indicates mortality or emigration of mature males. One would expect this to be most severe in a crowded population as the data indicate.

C. Fecundity and fertility

Fecundity, as used in this paper, refers to egg or sperm production ; fertility refers to the number of eggs developing into living embryos. Recognized criteria of fecundity are the presence of visible corpora lutea in females, and the presence of visible tubules in the cauda epididymis of males. Fertility is most conveniently expressed as the pregnancy rate and the average litter size.

TABLE 5

Fecundity : Percentages of fecund individuals. Sample sizes in parentheses.

	Low Density	Medium Density	High Density	Very High Density	Totals	Chi-Square[1]
Males						
12·6–17·5 gms.	92·3	90·6	83·8	84·9	86·97	6·3749
	(91)	(138)	(266)	(73)	(568)	
over 17·5 gms.	97·2	100	97·6	100	98·30	2·6430
	(36)	(64)	(164)	(31)	(295)	
Females						
12·6–17·5 gms.	98·5	93·6	87·9	83·7	89·94	11·2619*
	(65)	(109)	(223)	(80)	(477)	
over 17·5 gms.	100	100	100	100	100	
	(79)	(144)	(300)	(88)	(611)	

[1] Chi-Square based upon hypothesis of homogeniety within the weight groups. One asterisk indicates significance within the 5 per cent level.

Fecundity of both sexes in the weight class over 17·5 grams remained 97 per cent to 100 per cent at all densities studied (Table 5). In the weight class of 12·6 to 17·5 grams, the fecundity of both sexes declined moderately. The decline was approximately 15 per cent in the females and 8 per cent in the males. These relatively minor changes may have resulted from either altered weight-age relationships, or from actual changes in the age-maturation relationships.

Fertility displayed remarkably high levels throughout all seasons and densities. A total of 50·46 per cent of 1088 female mice over 12·6 grams were visibly pregnant at autopsy (Table 6). Between density classes,

TABLE 6

Fertility : Percentages of females with visible pregnancies (visible by autopsy). Sample sizes in parentheses.

Weight class	Low Density	Medium Density	High Density	Very High Density	Totals	Chi-Square[1]
12·6–17·5 gms.	40·0 (65)	37·6 (109)	34·5 (223)	23·8 (80)	34·17 (477)	5·3519
over 17·5 gms.	73·4 (79)	58·3 (144)	63·3 (300)	61·4 (88)	63·175 (611)	5·0632
Totals	58·3 (144)	49·4 (253)	51·0 (523)	43·4 (168)	50·46 (1088)	7·0018

[1] Chi-Square based upon hypothesis of homogeniety. Chi-Square necessary for significance at the 5 per cent level = 7·815.

pregnancy rates varied from 58·3 per cent in the low density populations, to 43·4 per cent in the very high density populations. These two figures in themselves attain Chi-square significance within the 5 per cent level.

D. Average litter sizes

The average litter sizes, based upon embryo counts in pregnant females, are given in Table 7. The overall average number of apparently viable embryos per pregnant female was 5·66 (based upon 549 pregnancies).

TABLE 7

Fertility : Average litter sizes (determined by embryo counts), and incidence of resorption.

	Low Density	Medium Density	High Density	Very High Density	Totals
Total average of all litters in each density class[1]	6·23	5·68	5·62	5·11	5·66
Standard error	±0·20	±0·15	±0.10	±0·20	±0·07
Sample size	(84)	(125)	(267)	(73)	(549)
Percentages of litters (pregnancies) with resorbing embryos	14·3	16·0	14·6	27·4[2]	16·575
Average number of resorbing embryos	1·6	2·2	1·7	2·0	1·9

[1] Analysis of variance on litter size means, F = 5·65 ; Probability = < 0·01.

[2] Chi-Square of this ratio, based upon hypothesis of homogeniety, = 6·3825 ; Probability (one degree of freedom) = < 0·02.

A significant decrease in litter size occurred with increasing population density. Eighty-four pregnancies in the lowest density class showed an average litter size of $6{\cdot}23 \pm 0{\cdot}20$, whereas seventy-three pregnancies in the highest density class showed an average litter size of $5{\cdot}11 \pm 0{\cdot}20$. This difference is not merely attributable to altered weight distribution patterns in the population.

E. Incidence of embryonic and foetal resorption

Of 549 pregnant females examined, 16·6 per cent contained at least one observable resorbing embryo or foetus (Table 7). Any conspicuously small and non-living embryo or foetus was counted as a resorption. The average number of resorbing embryos or foetuses per resorption female was 1·9. Three pregnancies were detected in which all visible embryos of the litter were being resorbed (the litter sizes involved were 1, 3 and 4).

The highest per cent of resorption, 27·4 per cent of seventy-three pregnancies, occurred in the highest density class. This is significantly above the average resorption percentage. No significant change in the number of resorbing embryos or foetuses per resorption female occurred.

F. Index of reproductive increase

The intrinsic rate of natural increase (" r ") would be a valuable statistic for comparisons between rick populations, but the data of this study do not permit the accurate calculation of " r ".

A simple index to reproductive rates may be obtained by the following method :

$$\text{Index of Repro. Increase} = \frac{\text{Total number of viable intrauterine young in population} + \text{Total number of preweaned yg. in population.}}{\text{Number of adult females}}$$

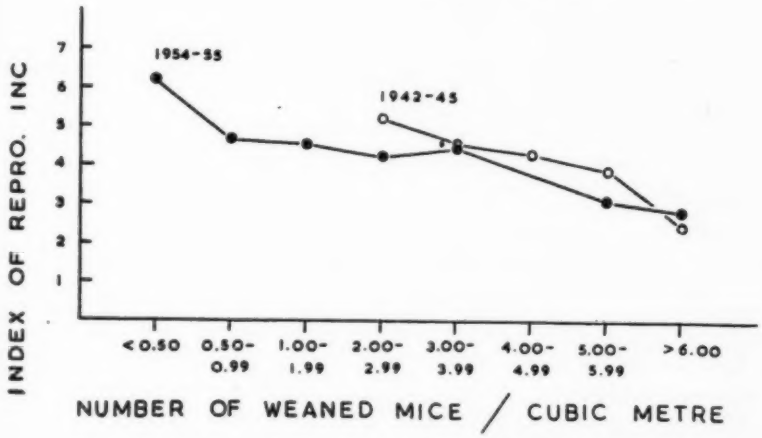

Fig. 2.—Index of reproductive increase. See text for explanation.

The resulting figure has no real meaning other than that of an index for comparative purposes. As such, however, it is superior to simple pregnancy rates, or simple birth rates as an indication of reproductive performance.

When this formula is applied to the data of this study, figures from 0·0 to 16·0 were obtained for individual populations. The averages of these figures throughout the various density classes are shown in Fig. 2. A progressive decline in the index of reproductive increase with increasing density is shown. The same statistic calculated for rick data obtained in 1942–45 by Southern & Laurie shows a fairly close agreement in level and trend.

G. Aggressive behaviour

The amount of aggressive behaviour within a population may be a significant factor in determining the demographic characteristics of the population. Behaviour observations are impossible on natural rick populations, but an index to aggressive behaviour is presented by the incidence of wounded mice.

TABLE 8

Incidence of wounded individuals. Percentages of conspicuously wounded or scarred individuals in total samples. (Sample sizes in parentheses).

	Low Density	Medium Density	High Density	Very High Density	Totals	Chi-Squares[1]
Females						
12·5–17·5 gms.	0 (65)	0 (109)	2·2 (223)	1·3 (80)	1·3 (477)	3·3764
over 17·5 gms.	0 (79)	2·1 (144)	1·7 (300)	2·3 (88)	1·6 (611)	2·5314
Totals	0	1·2	1·9	1·8	1·5	2·7900
Males						
12·5–17·5 gms.	0 (91)	4·3 (138)	6·4 (266)	11·0 (73)	5·5 (568)	10·1638*
over 17·5 gms.	2·8 (36)	7·8 (64)	28·7 (164)	45·2 (31)	22·7 (295)	29·1142**
Totals	0·8	5·4	14·9	21·1	11·4	25·2351**

[1] Chi-Square based upon hypothesis of homogeniety. One asterisk indicates significance within the 5 per cent level ; two asterisks, within the 1 per cent level.

Table 8 shows a greatly increased percentage of wounded males with increasing density. The percentage of wounded females remained basically unchanged.

This density-dependent behavioural response may provide a clue to certain demographic changes.

H. Adrenal weights

Recent studies of Christian (1955, 1956) have shown that the adrenal glands of house mice may undergo noticeable enlargement in crowded and socially

disrupted populations. Clark (1952) has demonstrated in the vole (*Microtus agrestis*) that fighting may produce enlargement of the adrenals and the spleen. These findings are in agreement with Selye's General Adaptation Syndrome, and they are now a generally accepted part of stress theory.

As an index to the physiological state of rick populations, samples of adrenal glands were taken from populations throughout the density range which was studied.[1] These data (weights of paired adrenals divided by two) are recorded in Table 9.

TABLE 9

Average adrenal weights (in milligrams) ± standard error. Sample sizes in parentheses.

	Low Density	Medium Density	High Density	Very High Density
Males				
7·6–12·5 gms.	1·8±0·11 (26)	1·8±0·09 (29)	1·5±0·07 (23)	1·4±0·16 (5)
12·6–17·5 gms.	2·3±0·08 (57)	1·9±0·10 (28)	2·0±0·06 (47)	2·0±0·14 (15)
over 17·5 gms.	2·6±0·10 (23)	2·6±0·12 (25)	2·3±0·08 (42)	2·7±0·13 (15)
Average of three Group Means	2·2	2·1	1·9	2·0
Females				
7·6–12·5 gms.	2·4±0·14 (39)	2·4±0·16 (29)	1·8±0·15 (22)	2·1±0·20 (5)
12·6–17·5 gms.	3·0±0·16 (40)	3·1±0·39 (16)	2·7±0·11 (33)	2·6±0·10 (5)
17·6–22·5 gms.	3·1±0·12 (35)	2·7±0·15 (31)	2·6±0·09 (42)	2·6±0·25 (5)
over 22·5 gms.	3·3±0·18 (11)	3·3±0·22 (9)	3·0±0·16 (30)	3·5±0·53 (5)
Average of four Group Means	2·9	2·9	2·5	2·7

The adrenal weights showed no enlargement in higher density classes; actually, a slight trend in the opposite direction is seen. Although fighting was known to occur in the dense populations, fighting of sufficient severity to wound 45 per cent of the adult males over 17·5 grams, it apparently did not produce adrenal hypertrophy.

[1] The glands were removed from the animals at autopsy, cleared of fat, and preserved in 4 per cent formalin. Prior to weighing, the glands were rinsed two to three minutes in two pans of clear water, and then laid on blotting paper for three minutes. Previous testing had demonstrated that this technique yielded results similar to weighing fresh glands. In fact, the technique standardized the weight of glands which had been subjected to varying periods of refrigeration.

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SUMMARY

This paper has presented certain demographic data of forty populations of house mice from English grain ricks. The populations are grouped into four density classes on the basis of the number of weaned mice per cubic metre. The resulting demographic averages of various density classes are then compared.

Relatively little reproductive alteration occurred in rick populations in relation to density. The major " density effects " so often observed in laboratory studies did not appear or were only moderately expressed in these data.

Mortality rates of the populations revealed no dramatic or conspicuous change throughout the density classes studied (as evidenced by weight ratios and sex ratios).

Fecundity of both sexes remained high throughout all density classes.

Fertility revealed a significant decline in the highest density class, but it still remained at high levels. Pregnancy rates declined from 58 per cent in the low density class to 43 per cent in the very high density class. Average litter size fell from 6·23 to 5·11.

Embryonic and fetal resorption increased significantly in the highest density class (14 per cent and 27 per cent).

The general rate of reproductive increase declined with increasing density.

The incidence of wounded males increased significantly in the highest density class (0·8 per cent to 21·1 per cent).

Adrenal weights did not reveal adrenal hypertrophy in crowded populations.

The relative stability of rick populations with increasing density is probably a reflection of the high quality of the habitat. Density effects are undoubtedly minimized by the favourable abundance and distribution of food and cover.

It is of equal interest that individual populations in this relatively uniform habitat did show wide variations in their population size and structure. The

fact that this variation is not obviously related to density, food, or cover, focuses attention on factors outside the normal realm of physical habitat as major population influences.

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A REVISION OF THE BRITISH ACEOSEJINAE (ACARINA: MESOSTIGMATA)

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[Accepted 10th December 1957]

(With 73 figures in the text)

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INTRODUCTION

In a recent publication on the British Mesostigmata (Evans, 1957), I outlined a new classification of a group of free-living mites which had previously been referred to the genera *Lasioseius* Berl., 1916 s.lat., *Arcoseius* Sig Thor, 1930, *Blattisocius* Keegan, 1944 and *Garmania* Nesbitt, 1951 s.lat. For key purposes, the group was considered to constitute the family Aceosejidae. The present work deals with a revision of the British members of one of the subfamilies, Aceosejinae, together with a synonymic list of species.

It has been found necessary to modify my original classification of the aceosejines as a result of a recent visit to the Berlese Collection at Florence where, through the kindness of the Director of the Stazione di Entomologia Agraria, I was able to figure a number of species of the *Lasioseius*-complex inadequately or erroneously described by Berlese. I have, however, retained my original concept of the subfamilial divisions although it appears to be of little phylogenetic significance.

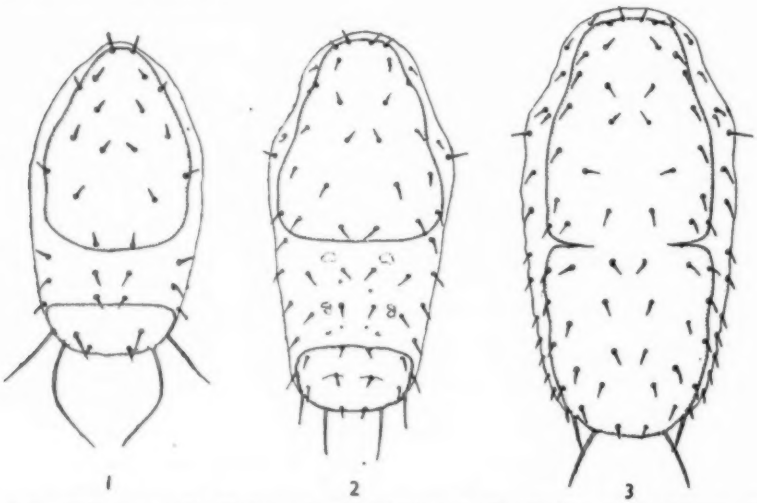
EXTERNAL MORPHOLOGY

The following account of the external morphology of the aceosejines deals chiefly with the adult stages since it was only in a few species that I was able to examine immature forms.

Chaetotaxy of the dorsal shield and lateral interscutal membrane

As in other free-living parasitoids, the anterior half of the dorsum of the larva is covered by a well-defined shield bearing nine pairs of setae (Fig. 1). The posterior half of the dorsum, is less heavily sclerotised but a pygydial shield bearing four or five pairs of setae and widely separated by striated cuticle from the anterior shield is usually present. The striated cuticle between these two shields carries five pairs of simple setae.

In all the protonymphal stages I have examined, the anterior shield, with an increased number of setae, and a pygydial shield are distinct (Fig. 2). Some species also have a number of small platelets on the striated cuticle between the two shields.



Figs. 1–3.—*Melichares agilis* Hering. 1. Chaetotaxy and sclerotisation of the dorsum of the larva. 2. Protonymph ; 3. Deutonymph.

The deutonymph is more heavily sclerotised than the preceding stages and often closely resembles the adult in general appearance. I have observed two types within the material at my disposal which differ in the form of the dorsal shield. In *Arctoseius*, *Leioseius*, *Melichares* (Fig. 3) and *Proctolaelaps* the dorsal shield has lateral incisions indicating the incomplete fusion of the anterior and posterior shield. This condition also occurs in the deutonymphs of the Macrochelidae, Pachylaelaptidae, and certain genera of the Laelaptidae. The second type (*Iphidozercon* and *Lasioseius*) has an entire dorsal shield, that is, without trace of incisions. In both types the marginal setae, when present, are situated on the lateral interscutal membrane. There is an increase in the number of setae during the development from the proto- to the deutonymph.

Since there is no addition of setae to the dorsum in the adult stage, the only significant difference between the chaetotaxy of the dorsum of the deutonymph and the adult is, in some species, the position of the marginal

series relative to the dorsal shield. The retention of the deutonymphal condition in which the marginal series is situated on the lateral interscutal membrane occurs in the majority of the aceosejines but in others, for example, members of the genus *Proctolaelaps*, the marginal series moves on to the shield so that the resulting chaetotactic pattern of the shield is markedly different from that of the deutonymph. In *Arctoseius* and *Leioseius* the incised dorsal shield of the deutonymph is retained in the adult stages whereas all other species have an entire dorsal shield.

Before proceeding with a more detailed account of the chaetotaxy of the dorsal shield of the adult stages, it is necessary to comment on the system of nomenclature adopted for the setae. On the basis of the post-embryonic development of the sclerotisation of the dorsum, it is possible to consider the dorsal shield of the adult as consisting of two shields, a notocephale and notogaster. The site of division of an entire dorsal shield into these two parts is based on the chaetotactic pattern of the shield and is indicated by a dotted line in all the figures of the dorsal shield given in this work. The dorsal setae may be considered to form four longitudinal rows on each side of the middle line. The eight rows on the posterior shield have been named according to the system introduced by Sellnick (1944) for the genus *Zercon*, namely, a dorsal series (J), a medial series (Z), a lateral series (S) and a marginal series (M). The latter is an addition to Sellnick's original system.

On this basis, the chaetotaxy and sclerotisation of the dorsum of the adult stages may be divided into the following four major types :

1. Dorsal shield with lateral incisions ; marginal series of setae on lateral interscutal membrane ..... *Leioseius*—type.
2. Dorsal shield entire ; without marginal series of setae in the region of the " posterior dorsal shield " ..... *Zercoseius*—type.
3. Dorsal shield entire ; marginal series of setae on lateral interscutal membrane ..... *Melichares*—type.
4. Dorsal shield entire ; marginal series of setae situated on the dorsal shield ..... *Proctolaelaps*—type.

Leioseius-type : this type is encountered in the genera *Leioseius* and *Arctoseius* and is characterised by the incision of the dorsal shield. The chaetotaxy of the shield and interscutal membrane is identical to that of the deutonymph. In *Leioseius*, the posterior dorsal shield (the region posterior to the lateral incisions) bears fifteen pairs of setae distributed as in Fig. 16. *Arctoseius*, on the other hand has only fourteen pairs on this region of the shield (Fig. 6).

Zercoseius-type : The genus *Zercoseius* differs from all other aceosejines in lacking a marginal series of setae in the region of the " posterior shield " (Fig. 28). The " posterior dorsal shield " carries fifteen pairs of setae arranged in three longitudinal rows of five setae on each side of the middle line.

Melichares-type : An entire dorsal shield with the marginal series situated on the interscutal membrane is probably the most common type encountered in the subfamily. It is seen in its least specialised form in *Melichares* (*M.*) *agilis* Hering (Fig. 45). There appears to be a tendency, in other species,

for the anterior setae of the series to fuse with the dorsal shield so that only two pairs of setae are situated on the interscutal membrane in the region of the anterior dorsal shield (Fig. 69). In *Lasioseius muricatus* (Koch) the fusion of the marginal setae with the anterior shield is complete (Fig. 68). One feature all these species have in common is that *there is no fusion of the marginal setae with the "posterior dorsal shield"*. Normally, there are fifteen pairs of setae on the posterior shield (Fig. 69) but in some species a reduction in number occurs as the result of the loss of one or more pairs in the dorsal series (Fig. 65).

Proctolaelaps-type : Species having the *Proctolaelaps*-type of dorsal chaetotaxy are undoubtedly closely related to the *Melichares*-type but differ in the extent to which the marginal series of setae is fused with the dorsal shield. In this group not only are the marginal series fused with the anterior shield but also form a longitudinal row along the margin of the "posterior shield" (Fig. 33). This results in the normal fifteen pairs of setae on the "posterior shield" of the *Melichares*-group being increased to twenty, twenty-one or twenty-two pairs in *Proctolaelaps*, depending on the number of marginal setae moving on to the shield.

Sclerotisation and chaetotaxy of the venter

The only areas of sclerotisation on the venter of the larva (excluding the tritosternum and gnathosoma) occur in the sternal and anal region. The sclerotisation of the sternal region is often difficult to discern. Only three pairs of sternal setae are present. The anal shield bears the normal three setae. There are no setae on the anal valves. Stigma, peritreme and peritrematal shield are not developed at this stage.

In the protonymph the sternal and anal shields are usually more heavily sclerotised than in the larva. The sternal region at this stage carries four pairs of setae (homologous with sternal setae I–III and the metasternals of the adult). The anal shield is essentially the same as in the larva. There is also an increase in the number of setae on the striated cuticle posterior to coxae IV and a pair of stigmata with short peritremes is present.

The venter of the deutonymph follows, in the main, the form seen in the protonymph. The chief differences between them is in the increased sclerotisation of the sternal region which bears five pairs of setae and in the elongation of the peritreme. Setae are also added to the region posterior to coxae IV.

The sclerotised structures on the venter of the female consist of a sternal shield usually bearing three pairs of setae, a pair of metasternal shields each with a seta, a wedge-shaped genital shield with or without a pair of setae, an anal or ventri-anal shield and, peritrematal and podal shields. The tritosternum with a rectangular base, longer than wide, and a pair of laciniae is present in all species. The range of variation in the form of these shields within the subfamily is summarised below :

(a) *Sternal and metasternal shields* : in certain species of the genera *Leioseius*, *Arctoseius*, *Proctolaelaps* and *Lasioseius* the sternal shield bears only two pairs of setae owing to the first pair being situated on jugularia (Figs. 17 and 42). The metasternal setae may be situated on the interscutal membrane in which case there are no metasternal shields.

(b) *Genital shield* : the typical wedge-shaped genital shield with a pair of setae is not developed in *Arctoseius* and *Iphidozercon*. In these genera the shield is narrow, parallel sided and without setae—the genital setae being situated on the striated cuticle lateral to the shield (Fig. 7).

(c) *Anal shield* : the retention of the deutonymphal type of anal shield occurs in *Iphidozercon*, *Proctolaelaps*, *Melichares*, etc. and in the majority of the species of *Arctoseius*. In the remaining genera, there is always fusion of the anal with the ventral shield resulting in a ventri-anal shield bearing a variable number of preanal setae. The cause of the increased sclerotisation of the anal region is not known but it is possible that increase in the size of the idiosoma or the size of the egg may be contributory factors.

(d) *Peritrematal shield* : this shield is usually well developed in all adult stages and may be free or fused with the expodal shield. The extent to which the anterior region of the shield is fused with the dorsal shield varies considerably throughout the group.

(e) *Podal shields* : these shields may be entire (Fig. 44) or fragmented (Fig. 42). They never appear to be fused between coxae II and III and III and IV. In the majority of species the endopodals are fused with the sternal shield.

The sclerotisation of the venter of the male is relatively constant throughout the group and consists of a sterniti-genital shield (usually bearing five pairs of setae) and a separate ventri-anal shield. The ventri-anal shield may be free or fused with the podal shields. In some species, there may be some indication of fusion of the sterniti-genital and ventri-anal shield. The genital orifice is presternal in position. Jugularia are not present in those species which have such shields in the female.

The gnathosoma

The form of the gnathosoma is essentially the same as in other free-living parasitoids. The chaetotaxy of the venter of the gnathosoma and the first three movable segments of the pedipalp shows the same pattern of development as I have shown in *Typhlodromus*—Evans, 1954. The arrangement of the setae on the venter of the gnathosoma is constant throughout the subfamily. The corniculi and salivary styli are well developed. The specialised seta on the inner basal angle of the palptarsus is typically two pronged. The tectum is extremely variable in form. In some species it has a smooth rounded anterior margin whilst in others the margin is produced into two, three or several tooth-like projections. The chelicerae are usually well developed with the digits dentate. In some of the females of *Melichares*, the fixed digit is reduced in length. The spermatophoral process is invariably conspicuous but not elaborate.

The legs

The legs are generally slender and consist of seven segments (including the pretarsus). All terminate in a lobed pulvillus and two claws. Tarsus IV in a few species is provided with a macroseta. With the exception of a little known genus *Hoploseius*, in which leg II of the female (the only known sex) is armed, there is little evidence of sexual dimorphism affecting the form of leg II.

CLASSIFICATION

It is apparent from the above account of the external morphology of the aceosejines that the chaetotaxy of the dorsum and degree of sclerotisation of the venter in the female provide suitable characters for the classification of the subfamily. The degree of sclerotisation of the venter in the female has been widely used in the classification of the Mesostigmata at generic and familial level and there is some justification for this since in most samples of terrestrial Parasitoidea, this sex greatly outnumbers the immature stages and males. Further, such " key characters " as the presence or absence of jugularia, or the degree of sclerotisation of the genital and anal regions are readily recognisable and provide the basis for a practical classification. The disadvantage of such a classification lies in the fact that not only is the identification of the species restricted to one sex but there is a tendency to exaggerate the importance of minor differences between species. This is only too obvious in the existing classification of the suborder which has been divided into a number of superfamilial groups on the basis of the sclerotisation of the genital region of the female.

Recent studies on the ontogeny of the Mesostigmata have shown that the development of the chaetotaxy and sclerotisation of the dorsum, and the chaetotaxy and structure of the gnathosoma are fundamental in the classification and are likely to provide more stable characters for a natural arrangement of the species in the suborder than those characters used at present. I have, therefore considered in the generic classification of the aceosejines the characteristics of the immature stages, as far as the material at my disposal permits, as well as those of both adult stages.

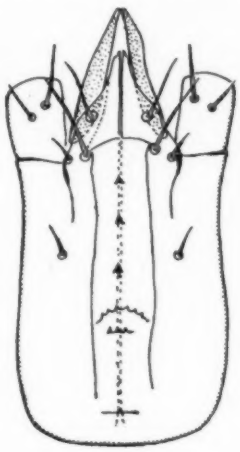
On the basis of the structure of the dorsal shield and its chaetotaxy, the adult stages may be divided into the following groups :—

1. Species in which the incised dorsal shield of the deutonymph is retained in the adult.
2. Species in which the dorsal shield in the adult is entire although it may be incised in the deutonymph.

The first group contains the genera *Arctoseius* and *Leioseius*. In the adult stages these genera may be separated by the chaetotaxy of the " posterior dorsal shield ". The sclerotisation of the venter of the females of the two genera also differ considerably and may be used as an additional character in their separation.

In the second and larger group, my generic concept differs radically from that of Berlese (1916) in which he considered the form of the dorsal setae to be an important criterion in classifying this group of species (*Lasioseius* sensu Berlese). I have considered three possible " characters ", namely, the sclerotisation of the venter of the female, the chaetotaxy of the dorsal shield and the form of the gnathosoma. The first has been rejected because no clear-cut differences could be observed between the species, for example, the sclerotisation of the anal region which has been used in previous classifications of the group, shows every gradation from a single anal shield to a ventri-anal shield with six pairs of pre-anal setae. Although the chaetotaxy of the dorsum is surprisingly constant, the position of the setae relative to the dorsal shield

enables the adult stages of the species to be readily divided into two groups. In the *Melichares*-group which includes the genera *Melichares* s. lat., *Iphidozercon*, *Lasioseius* and *Zercoseius* the marginal series (M), when present, never occurs on the " posterior dorsal shield " so that the number of setae on it never exceeds fifteen pairs. The genus *Proctolaelaps*, on the other hand, has from four to six pairs of marginal setae on the lateral margins of the " posterior dorsal shield " resulting in its bearing nineteen or more setae. There appears to be no correlation between the increased setation of the dorsal shield and the



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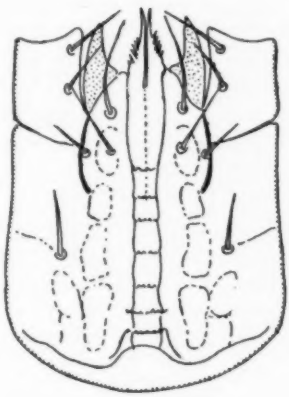

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Fig. 4.—Venter of the gnathosoma of *Melichares agilis* Hering.
Fig. 5.—Venter of the gnathosoma of *Lasioseius berlesei* (Oudemans).

degree of sclerotisation of the venter of the female. The division of the *Melichares*-group into genera has as its basis the form of the " rostrum " (*cf.* Figs. 4 and 5), the number of setae on the " posterior dorsal shield " and the dentition of the fixed digit of the chelicera.

The following key to the genera of the adult stages of the Aceosejinae is based not only on the examination of British species but also on a large collection of extra-Palaearctic species in the collections of the British Museum (Natural History).

Key to genera and subgenera of the adult stages of the British Aceosejinae.

1.	Dorsal shield in both sexes with lateral incisions (Fig. 6).	2.
–.	Dorsal shield in both sexes with lateral margins entire ..	3.
2.	Region of the dorsal shield posterior to the incisions with 14 pairs of setae (Fig. 6) ; genital shield in the female narrow, without setae ; female usually with anal shield	*Arctoseius* Sig Thor (p. 184).
–.	Region of the dorsal shield posterior to the incisions with 15 pairs of setae (Fig. 16) ; genital shield with setae ; female with ventri-anal shield	*Leioseius* Berlese (p. 189).

3. Both sexes lacking a marginal series of setae in the region of the " posterior dorsal shield " (Fig. 28) ; setae, at least in the posterior half of the shield, leaf- or feather-like ; female with ventri-anal shield ..... *Zercoseius* Berlese (p. 195).
–. Both sexes with a marginal series of setae in the region of the " posterior dorsal shield " (Figs. 33 and 54) .... 4.
4. Marginal series situated on the lateral margin of the " posterior dorsal shield " so that this region of the shield bears nineteen or more pairs of setae (Fig. 33) *Proctolaelaps* Berlese s. lat. (p. 197)
(a) Peritrematal shields free posteriorly ; female with an anal shield, anal opening usually enlarged (Fig. 31) *Proctolaelaps* s. str.
–. Peritrematal shield fused with the expodal shield posteriorly ; female with a ventri-anal shield, anal opening normal (Fig. 42)..... *Neojordensia* Evans.
–. Marginal series in the region of the " posterior dorsal shield " free and situated on the lateral interscutal membrane ; " posterior dorsal shield " with never more than fifteen pairs of setae (Fig. 54) ..... 5.
5. Corniculi long and slender, convergent and lying very close to each other ; transverse rows of denticles in the ventral groove of the gnathosoma often reduced (Fig. 4). Idiosoma usually weakly sclerotised ..... *Melichares* Hering s. lat.
(a) Females with an anal shield (Fig. 46) ..... *Melichares* s. str. (p. 207).
Females with a ventri-anal shield (Fig. 51) ..... *Blattisocius* Keegan (p. 208).
–. Corniculi relatively short, more or less parallel and well-separated distally (Fig. 5) ; ventral groove with 5 or more transverse rows of denticles ..... 6.
6. " Posterior dorsal shield " with 14 pairs of setae, J series always comprising 5 pairs of setae (Fig. 57) ; genital shield in the female without setae ; female usually with an anal shield ; sternal shield narrow, not fused with the endo-podals ; fixed digit of the chelicera without a row of closely-set teeth along its cutting edge ..... *Iphidozercon* Berlese (p. 212).
–. " Posterior dorsal shield " normally with 15 pairs of setae (Fig. 69) when fewer setae present the J series with less than 5 pairs of setae (Fig. 65) ; genital shield with setae; female with ventri-anal shield ; sternal shield broad and fused with exopodal shield ; fixed digit of the chelicera usually with a row of closely-set teeth along its cutting edge ..... *Lasioseius* Berlese (p. 215).

Genus *ARCTOSEIUS* Sig Thor.

Arctoseius Thor, Sig (1930). Skr. Svalbard Ishavet Oslo **27** : 122 ; Willmann, C. (1949). Abh. naturw. Ver. Bremen **32** : 348 ; Evans, G. O. (1955). Bull. Brit. Mus. (nat. Hist.) Zool. **2** (9) : 287.
Tristomus Hughes, A. M. (1948). Mites associated with stored food products. H.M.S.O. London : 138.
Arctosciulus Willmann, C. (1949). Abh. naturw. Ver. Bremen **32** : 357 *syn. nov.*
Arctotarseius Willmann, C. (1949). . . tom. cit. . . . . : 357 *syn. nov.*

Type : *Arctoseius laterincisus* Sig Thor (1930)

All the known species of this genus are small free-living mites which have the dorsal shield incised laterally in the deutonymphal and adult stages. The dorsal shield bears thirty-one pairs of simple setae of which fourteen pairs

are situated posterior to the lateral incisions. The marginal series is situated on the lateral interscutal membrane. In the female, the sternal shield normally has three pairs of setae but in some species the first pair is situated on jugularia. The sclerotisation of the anterior margin of the sternal shield is often difficult to discern. Some species have pre-endopodal shields. The metasternal setae are free and situated on the integument. The endopodal shields are usually weak and not fused with the sternal shield. The genital shield is narrow and without setae. With the exception of *Arctoseius magnanalis* sp. n., the anal shield bears only the normal three setae ; in *magnanalis*, however, the increased sclerotisation of the anal region has resulted in the shield incorporating one pair of ventral setae. The metapodal shields are conspicuous and generally elongate in form. The length of the peritreme varies considerably throughout the genus—in some species it does not extend beyond the anterior margin of coxa II. The degree of fusion of the peritrematal shield with the dorsal shield also varies considerably.

The sclerotisation of the venter of the male is relatively constant and consists of a sterniti-genital shield bearing four or five pairs of setae and a separate ventri-anal shield.

The form and chaetotaxy of the gnathosoma is normal for the subfamily. The corniculi are relatively short and widely separated distally. The tectum is bi- or tridentate. The movable digit of the chelicera is usually bi-dentate but the dentition of the fixed digit varies from two or three well-separated teeth to a row of small closely-set teeth. The spermatophoral process is usually simple.

All legs usually terminate in a lobed pulvillus with two claws although in some species the pulvillus on tarsus I is reduced. The distal third of tarsus I has rod-like or clubbed setae.

The most comprehensive study on *Arctoseius* is that by Willmann (1949) in which he divided the females of the genus into four subgenera on the basis of the sclerotisation of the anterior region of the sternal shield, the chaetotaxy of tarsus I and the form of the shield surrounding the anus. His subgeneric concept may be summarised as follows :

1. Females with ventri-anal shield ..... (Type : *Arctoseius ibericus* Willmann).	*Arctosciodes* Willmann.
–. Females with an anal shield	2.
2. Jugularia present ..... (Type : *Laelaps semiscissus* Berl.).	*Arctoseiulus* Willmann.
–. Jugularia absent but pre-endopodal shields may be present	3.
3. Tarsus I with conspicuous rod-like or clubbed sensory setae .. (Type : *Arctoseius austriacus* Willmann).	*Arctotarseius* Willmann.
–. Tarsus I without conspicuous rod-like or clubbed setae.....	*Arctoseius* s. str.

The subgenus *Arctoseiodes* shows greater affinity to *Leioseius* than to *Arctoseius* and its systematic position will be discussed below (p. 190). The characters separating the other two subgenera from *Arctoseius* s.str., although presenting good " key characters ", do not warrant the importance attributed to them by Willmann. For example, the sclerotisation of the anterior region of the sternal shield is so variable throughout the genus that

other combinations are possible. The separation of *Arctotarseius* from *Arctoseius* s.str. is simply based on the degree of development of the sensory setae on tarsus I. All species have rod-like setae on the tarsus but it is only in *austriacus* (=*Gamasellus* (*Sessiluncus*) *eremita* Berlese) and to a lesser degree *Arctoseius pannonicus* Willmann, that they are enlarged and conspicuous. In view of this I am relegating *Arctoseiulus* and *Arctotarseius* to the synonymy.

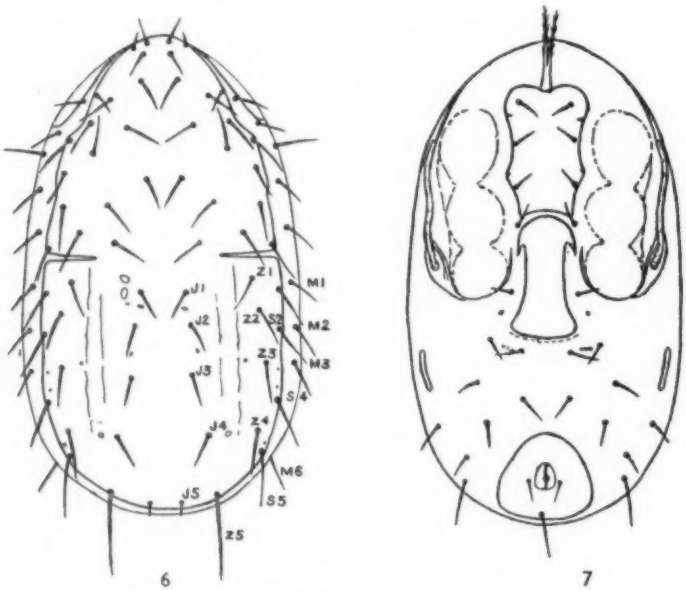
At present, there are only four species of *Arctoseius* known in Britain. The females may be distinguished as follows :

Key to the females of British species of Arctoseius *Sig Thor*

1. Tectum bispinate ; peritreme extending as far as the middle of coxa II (Fig. 7)	*A. cetratus* (Sellnick).
–. Tectum trispinate ; peritreme extending beyond coxa I	2.
2. With a ventri-anal shield bearing one pair of preanal setae (Fig. 11)	*A. magnanalis* sp. n.
–. With anal shield	3.
3. Pre-endopodal shield well-sclerotised, distinct, sternal shield completely ornamented (Fig. 8)	*A. pannonicus* Willmann,
–. Without pre-endopodal shields, sternal shield weakly ornamented (Fig. 9)	*A. butleri* (Hughes).

ARCTOSEIUS CETRATUS (Sellnick)

Lasioseius cetratus Sellnick, M. (1940). Goteborgs. Vetensk. Samh. Handl. (5) **6B** : 99, figs. ; Schweizer, J. (1949). Rés. Rech. scient. Parc Nation. Suisse **2** (N.S.) : 53, figs.
Arctoseius bispinatus Weis-Fogh, T. (1947). Nat. Jutlandica **1** : 225, figs.



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Figs. 6–7.—*Arctoseius cetratus* (Sellnick), female. 6. Dorsum ; 7. Venter.

The following redescription of *cetratus* is based on specimens collected in Iceland (the type locality) by Dr Tuxen, Copenhagen.

Female. Dorsal shield (340–360 × 150–155 μ) with strong lateral incisions and bearing thirty-one pairs of simple setae distributed as in Fig. 6. Z5 considerably longer than the other dorsal setae.

Sternal shield narrow, with three pairs of setae (Fig. 7). Metasternals free on integument. Genital shield without setae. Anal shield about as broad as long but variable in outline. Paranals slightly more than one-half the length of the postanal seta. Metapodal shields slender ; integument posterior to coxae IV and eight pairs of setae. Peritrematal shield fused with the exopodal shield in the region of coxae IV but free anteriorly. Peritreme extending as far as the middle of coxa II.

Gnathosoma normal for genus ; corniculi short, not extending beyond the anterior margin of the palptrochanter. Tectum bispinate (length of the processes and their distance apart variable). Movable digit of the chelicera bidentate ; fixed digit with six or seven small teeth.

Sensory setae on tarsus I not enlarged. All tarsi with claws.

Distribution. This species has been recorded from Iceland (Sellnick, 1940) ; Denmark (Weis-Fogh, 1947), Switzerland (Schweizer, 1949) and Britain (Evans, 1954). The record of *Arctoseius halophilus* Willmann given by Evans (1954) is based on a misidentification—the species is *A. cetratus*.

ARCTOSEIUS BUTLERI (Hughes)

Tristomus butleri Hughes, A. M. (1948). Mites associated with stored food products. H.M.S.O. London : 138, figs.

Arctoseius butleri, Evans, G. O. (1954). Bull. Brit. Mus. (nat. Hist.) Zool. **2** (9) : 288.

This species bears a superficial resemblance to *A. pannonicus* but may be readily distinguished from that species by the structure and ornamentation of the sternal shield. In *butleri* there are no pre-endopodal shields and the

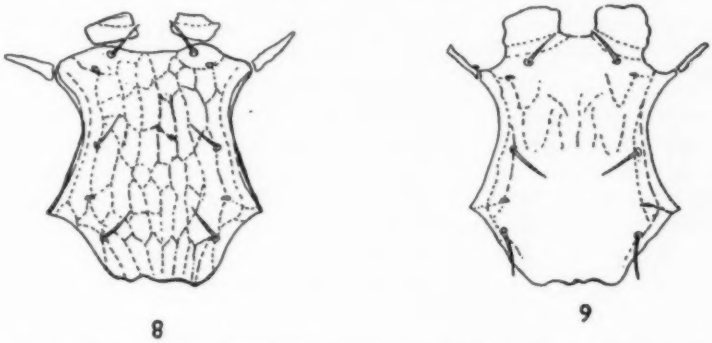

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Fig. 8.—*Arctoseius pannonicus* Willmann, female. Sternal shield. 9. *Arctoseius butleri* (Hughes), female. Sternal shield.

ornamentation of the shield is weak (Fig. 9). The form and chaetotactic pattern of the dorsal shield is typical of the genus.

Distribution. At present, this species is known only from the type locality —Belfast, Northern Ireland (Hughes, 1948).

ARCTOSEIUS PANNONICUS Willmann

Arctoseius pannonicus Willmann, C. (1949). Abh. naturw. Ver. Bremen, **32** : 353, figs.

The original description and figures of this species are adequate for its identity. The dorsal shield bears thirty-one pairs of short setae. Those on the posterior half of the shield are longer than figured by Willmann. The ornamentation of the sternal shield and the form of the pre-endopodal shields are shown in Fig. 8.

Distribution. The type material was collected in Austria. I have examined specimens from : litter under Box trees, Box Hill, Surrey (1956 : 1 : 18 : 4–13) and from leaf mould at Ruislip, Middlesex (1954 : 3 : 15 : 1).

ARCTOSEIUS MAGNANALIS, sp. n.

Female : Dorsal shield (approx. $450 \times 242\,\mu$) with strong lateral incisions and the usual thirty-one pairs of simple setae distributed as in Fig. 10. Surface of the shield with faint reticulations and minute punctures. Lateral interscutal membrane with nine pairs of setae.

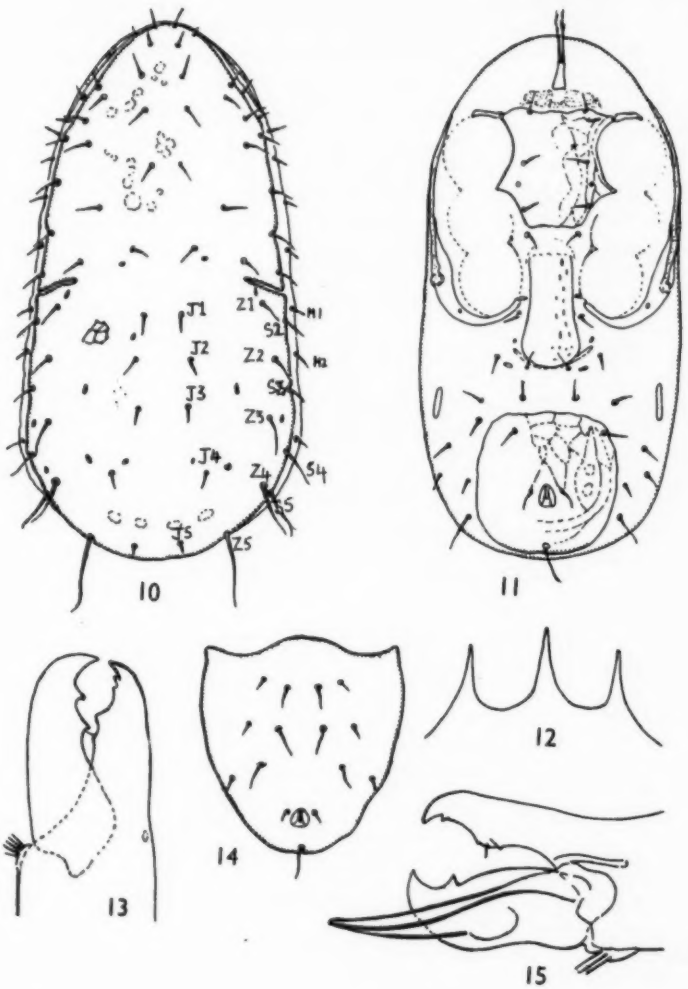
Venter with well-sclerotised shields. Sternal shield reticulated and with three pairs of setae. Integument anterior to the shield with traces of sclerotisation as indicated in Fig. 11. Genital shield narrow, gently rounded posteriorly and punctured ; without genital setae. Ventri-anal shield ($132 \times 121\,\mu$) with a pair of preanal setae ; anal setae about one-half the length of the postanal seta. Metapodal shields elongate ; small shields present posterior to the genital shield. Integument posterior to coxae IV with eight pairs of setae. Peritrematal shield fused with dorsal shield anteriorly and produced posterior to coxa IV. Peritreme extending beyond coxa I.

Gnathosoma normal for the genus with the tectum trispinate (Fig. 12). The movable digit of the chelicera is bidentate and the fixed tridentate (Fig. 13).

The sensory setae on tarsus I are not enlarged although a long tactile seta, clavate at its distal end, is present. All legs are provided with ambulacra.

Male. The chaetotaxy of the incised dorsal shield ($385 \times 220\,\mu$) is essentially the same as in the female. The venter is almost entirely covered by a sterniti-genital shield bearing five pairs of setae and a ventri-anal shield with six pairs of preanal setae (Fig. 14). The three inner pairs of preanal setae are about twice the length of the externals. The ventri-anal is not fused with the well-developed peritrematal shield. The genital orifice is presternal. Gnathosoma as in the female. Movable digit of the chelicera unidentate and with a simple spermatophoral process ; fixed digit with three or four small teeth (Fig. 15). Leg II unarmed.

Distribution. Three specimens collected by M. E. Bacchus from flood debris, Rydal Water, Westmorland (Holotype ♀ : 1957 : 11 : 22 : 22 ; Allotype ♂ : 1957 : 11 : 22 : 23 and Paratype : 1957 : 11 : 22 : 24). A single female from humus and soil under Oak in Roudsea Wood, North Lancashire, collected J. Satchell (Paratype : 1957 : 11 : 22 : 25).



Figs. 10–15.—*Arctoseius magnanalis* sp. n. 10. Dorsum of female ; 11. Venter of female ; 12. Tectum of female ; 13. Chelicera of female ; 14. Ventri-anal shield of male ; 15. Chelicera of male.

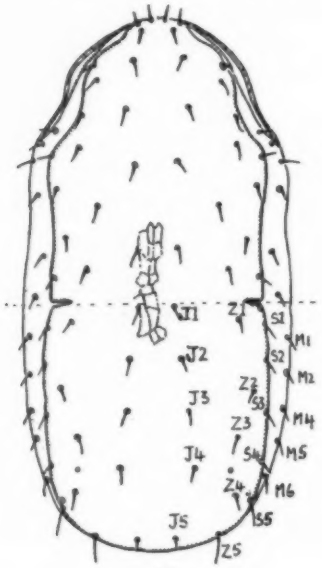
Genus *LEIOSEIUS* Berlese

Leioseius Berlese, A. (1916). Redia **12** : 45.
Arctoseiodes Willmann, C. (1949). Abh. naturw. Ver. Bremen **32** : 357 *syn. nov.*

Type : *Ameroseius minusculus* Berlese, 1905

The adult stages of this genus show a superficial resemblance to those of the genus *Arctoseius* in retaining the incised dorsal shield of the deutonymph.

Species of the two genera are readily distinguished, however, on the basis of the chaetotaxy of the dorsal shield behind the incisions—*Arctoseius* having fourteen pairs of setae and *Leioseius* fifteen pairs. The lateral interscutal membrane, with the exception of *Leioseius ibericus* (Willmann), bears eleven or twelve pairs of setae (Fig. 16). The sternal shield in the female is usually strongly sclerotised and bears two or three pairs of setae. In those species with two pairs of setae on the sternal shield, the first pair of sternal setae are situated on jugularia or on the striated membrane anterior to the shield. The genital shield is wedge-shaped and is provided with the normal pair of setae. A ventri-anal shield is present in both sexes.



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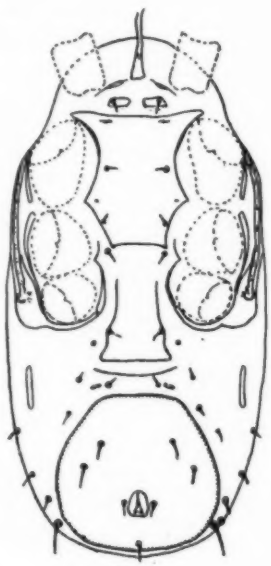

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Figs. 16–17.—*Leioseius minusculus* (Berlese), female. 16. Dorsum ; 17. Venter.

The gnathosoma is normal for the family with the chelicerae chelate-dentate and the tectum trispinate. All legs have ambulacra.

There is little doubt that *L. ibericus* is atypical of the genus in the chaetotactic pattern of the dorsal shield and lateral interscutal membrane. Although the region of the dorsal shield posterior to the incisions bears fifteen pairs of setae not all these are homologous with the same number of setae on the region of the shield in other species of the genus (cf. Figs. 16 and 20). In view of the similarity between *ibericus* and other known species of the genus in other characters, e.g. sclerotisation of the venter and gnathosoma, I am provisionally including the species in *Leioseius*.

Three species of the genus occur in Britain. *L. minusculus*, although not recorded from Britain, is included in the following key for comparative purposes.

Key to the species of the genus Leioseius

Females

1. First pair of sternal setae on the sternal shield (Fig. 21); vertical setae spinose; with only four pairs of marginal setae on the lateral interscutal membrane. Associated with *Balanus* ..... *L. ibericus* (Willmann).
–. With the first pair of sternal setae on jugularia or on the striated membrane anterior to the sternal shield; verticle setae simple; lateral interscutal membrane with eleven or twelve pairs of setae ..... 2.
2. Ventri-anal shield with eleven setae (Fig. 19); with six platelets between the genital and the ventri-anal shield *L. salinus* Halbert.
–. Ventri-anal shield with seven or nine setae on the ventri-anal shield; never with six platelets between the genital and ventri-anal shield ..... 3.
3. Dorsal shield scabrid; first pair of sternal setae on the membrane (Fig. 27); ventri-anal shield with nine setae; anterior pair of preanals relatively close to the anterior margin of the shield; ventri-anal shield about one and a half times as broad as long..... *L. elongatus* sp. n.
–. Dorsal shield reticulated but not scabrid; first pair of sternal setae on jugularia; ventri-anal shield with seven setae, anterior pair of preanals widely removed from the anterior margin of the shield (Fig. 17); ventri-anal shield about as broad as long ..... *L. minusculus* (Berlese).

Males

1. Spermatophoral process on the movable digit of the chelicera strongly incurved distally ..... *L. minusculus* (Berl.).
–. Spermatophoral process straight ..... 2.
2. With marginal series on the membrane in the region of the "posterior dorsal shield"; ventri-anal shield with fifteen setae ..... *L. salinus* Halbert.
–. Without marginal on the membrane lateral to the "posterior dorsal shield"; ventri-anal shield with seven setae ..... *L. ibericus* (Willmann).

LEIOSEIUS MINUSCULUS (Berlese)

Ameroseius minusculus Berlese, A. (1905). Redia **2**: 235.
Lasioseius (*Leioseius*) *minusculus* Berlese, A. (1916). Redia **12**: 45.

Female. The reticulated dorsal shield (approx. 380 × 175 μ) is provided with thirty-two pairs of simple setae distributed as in Fig. 16. The lateral incisions are conspicuous. The lateral interscutal membrane bears eleven pairs of setae.

The jugularia are weakly sclerotised and lie between the anterior margin of the sternal shield and a pair of small pre-endopodal shields (Fig. 17). The sternal shield has only two pairs of setae; the metasternals lie on the membrane The wedge-shaped genital shield with a pair of setae is separated from the ventri-anal shield by striated cuticle bearing two pairs of setae. The ventri-anal shield, almost as long as broad, has two pairs of preanal setae. The anterior pair of preanals is widely removed from the anterior margin of the shield. The exopodal shields are fragmented but the peritrematal shield is well developed with the peritreme extending beyond coxa I.

Gnathosoma normal, tectum trispinate. Chelicera with the fixed digit multidentate.

Male. The sclerotisation and chaetotaxy of the dorsum is essentially the same as in the female. The dorsal shield measures about 310 × 132 μ.

The sterniti-genital shield bears five pairs of setae—there are no jugularia. The ventri-anal (110 × 125 μ) has fifteen setae.

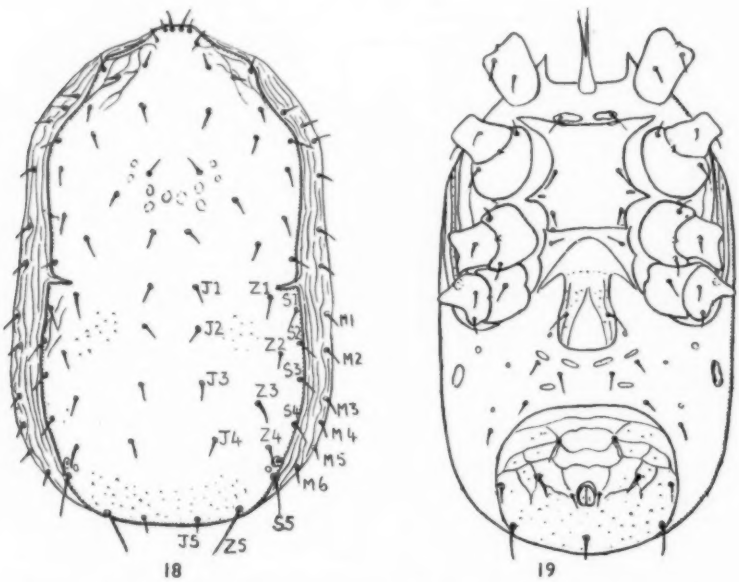
The gnathosoma is similar to that in the female. The movable digit of the chelicera has the spermatophoral process considerably longer than the digit; the process is strongly incurved distally. Leg II is unarmed.

Distribution. The above redescription of the species is based on the examination of the type material in the Berlese Collection at Florence. The type locality is given as " . . . sub foliis emortuis ad paludes in Italia boreale (" Undine ")". I have recently examined specimens of both sexes of this species from soil in an orchard, Storrs, Connecticut, U.S.A. (Coll. H. Hurlbutt). The male described by Schweizer (1949) under the name *Leioseius minusculus* (Berl.) is a male of *Typhlodromus* sp.

LEIOSEIUS SALINUS (Halbert)

Lasioseius salinus Halbert, J. N. (1920). Proc. Roy. Irish Acad. **35** : 125 fig.

Female. Dorsal shield (approx. 440 × 260 μ) with minute punctures and shallow lateral incisions (Fig. 18); with thirty-two pairs of setae of which fifteen pairs occur on the region posterior to the incisions. The lateral interscutal membrane bears twelve pairs of setae.



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Figs. 18–19.—*Leioseius salinus* (Halbert), female. 18. Dorsum; 19. Venter.

Ventrally, the jugularia are conspicuous ; the sternal shield having only two pairs of setae. The metasternals are situated on the striated membrane posterior to the sternal shield (Fig. 19). The punctured genital shield has the usual pair of setae and is separated from the ventri-anal shield by a relatively wide expanse of membrane carrying three pairs of setae and six platelets. The ventri-anal shield (approx. 132 × 170 μ) minutely punctured and bearing eleven simple setae. The expodal shields are entire and the peritrematal and metapodal shields well developed.

The gnathosoma is normal for the subfamily with the tectum produced into three processes. The movable digit of the chelicera is bidentate and the fixed has about four weaker teeth. All legs have well-developed ambulacra.

Male. The ornamentation and chaetotaxy of the incised dorsal shield (approx. 330 × 185 μ) is essentially the same as in the female except in the fusion of two anterior pairs of marginal setae with the shield.

The geniti-ventral shield carries five pairs of setae. There are no jugularia. The ventri-anal shield (approx. 127 × 160 μ) bears fifteen setae. The spermatophoral process is considerably longer than the digit but is not incurved distally as in *L. minusculus*. Leg II is unarmed.

Distribution. The type locality of this species is " under dead shells in a salt marsh on Malahide Island ". Willmann (1952) records it from the island of Wangerooge and there are specimens of both sexes in the British Museum (Natural History) from a salt-marsh in Carmarthenshire, South Wales (Coll. R. Howells).

LEIOSEIUS IBERICUS (Willmann)

Arctoseius ibericus Willmann, C. (1949). Abh. Naturw. Ver. Bremen **32** : 356.
Arctoseius (*Arctoseiodes*) *ibericus* Willmann, C. (1949). tom. cit.: 357.

Female. Dorsal shield (465 × 245 μ) with strong lateral incisions and thirty-three pairs of setae distributed as in Fig. 20. " Posterior dorsal shield " with fifteen pairs of setae of which Z3–Z5 are considerably longer and stronger than the other setae. There are no setae on the membrane lateral to the " posterior dorsal shield ". There are only four pairs of setae in the J series.

The pre-endopodal shields are conspicuous and the sternal shield bears three pairs of short setae (Fig. 21). The metasternals are free on the integument. The genital shield is rectangular in form with its posterior margin slightly convex. Between the genital and ventri-anal shields lie six platelets and a pair of setae. The ventri-anal has three pairs of pre-anals. The form of the metapodalia and the chaetotaxy of the region posterior to coxae IV are shown in the figure.

Gnathosoma with relatively short, stout corniculi. Tectum trispinate (Fig. 22). Fixed digit of the chelicera with four teeth ; movable digit bidentate (Fig. 23).

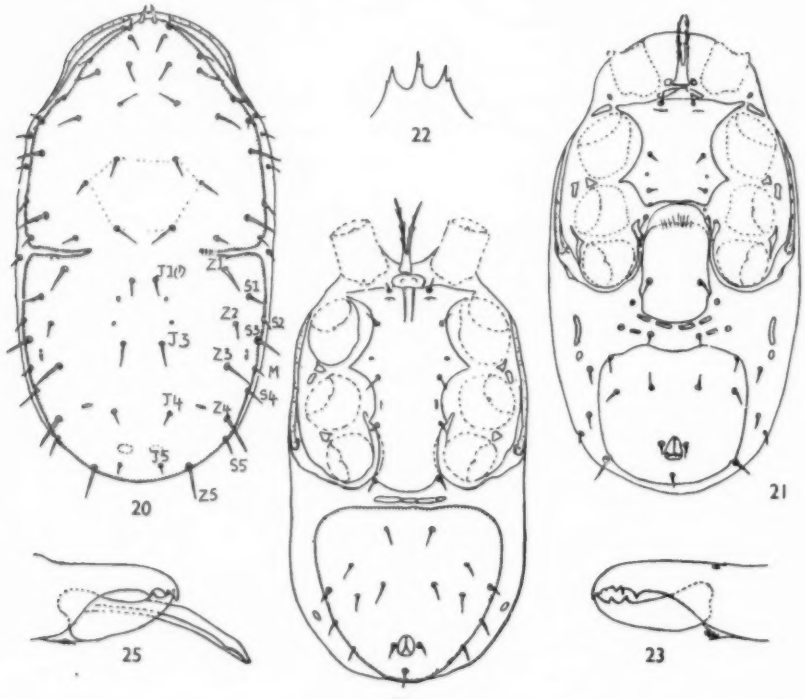
All legs with pretarsi and ambulacra.

Male. Dorsal shield with thirty-five pairs of setae due to the fusion of two pairs of setae situated on the lateral interscutal membrane in the female with the dorsal shield. Relative lengths of the dorsal setae as in the female.

Sterniti-genital shield with five pairs of setae. Ventri-anal shield with 17 setae (Fig. 24). Platelets present between sterniti-genital and ventri-anal shield. Podal and peritrematal shields as in the female.

Fixed digit of the chelicera tridentate ; movable unidentate (Fig. 25). Spermatophoral process simple.

Distribution. The type habitat is given as : " Spanien, Quelle bei San Sebastian am Strande ". I have examined specimens of both sexes, collected by J. Hobart, from the seashore at Plymouth, Devonshire and Nevin, Caernarvonshire. In both localities, the species was associated with *Balanus*.



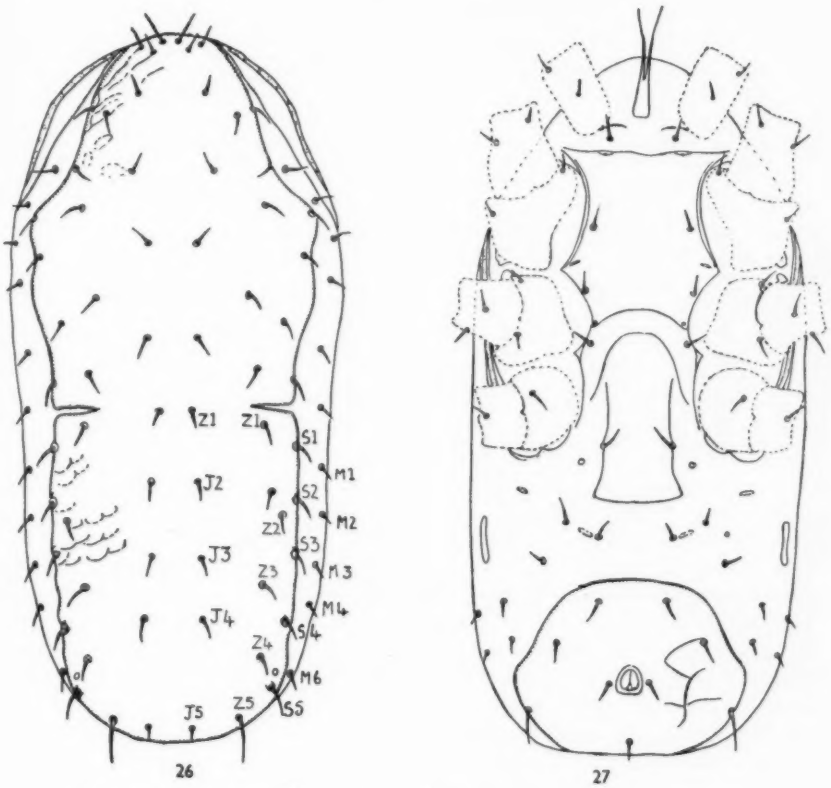
Figs. 20–25.—*Leioseius ibericus* (Willmann). 20. Dorsum of female ; 21. Venter of female ; 22. Tectum of female ; 23. Chelicera of female ; 24. Venter of male ; 25. Chelicera of male.

LEIOSEIUS ELONGATUS, sp. n.

Female. Dorsal shield scabrous, 410 μ in length and 160 μ in breadth, with thirty-two pairs (excluding an unpaired seta present anterior to Z2 on the right side of the " posterior dorsal shield ") of setae distributed as in Fig. 26. Lateral incisions conspicuous. Bases of setae S3–S5, Z4–Z5 and J4–J5 on slight elevations.

Sternal seta I on the striated integument anterior to the sternal shield bearing two pairs of setae (Fig. 27). Metasternal setae free. Wedge-shaped

genital shield with a pair of setae and widely separated from the ventri-anal shield (98 × 130 μ). Ventri-anal shield with nine setae ; bases of anterior preanals lying relatively close (11–13 μ) to the anterior margin of the shield. Integument between genital and ventri-anal shield with a pair of weakly sclerotised platelets. Metapodalia long and slender.



Figs. 26–27.—*Leioseius elongatus* sp. n., female. 26. Dorsum ; 27. Venter.

Gnathosoma normal for the genus. Tectum produced into three stout processes, each process denticulate distally. Fixed digit of the chelicera with a row of small teeth ; movable digit apparently bidentate.

All legs with pretarsi and ambulacra.

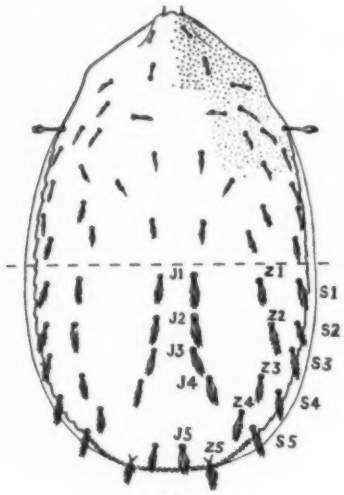
Locality. A single female (Holotype : 1957 : 11 : 22 : 7) from Beech litter, Box Hill, Surrey (Coll. K. H. Hyatt, 1953).

Genus *ZERCOSEIUS* Berlese

Zercoseius Berlese, A. (1916). Redia **12** : 43.

Type : *Seius spathuliger* Leonardi, 1899

The type and only known species of this genus differs from other species considered in this work in lacking a marginal series of setae in the chaetotaxy of the posterior half of the dorsum. The dorsal shield in both sexes is entire and bears thirty-four pairs of serrate or plumose setae. The " anterior dorsal shield " bears nineteen pairs distributed as in Fig. 28. The distribution of the fifteen pairs on the " posterior dorsal shield is normal. "



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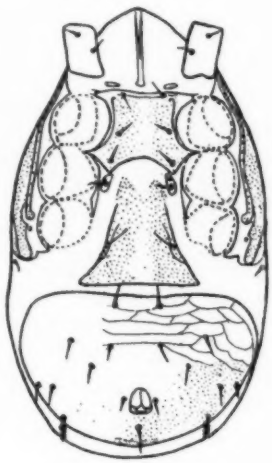

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Figs. 28–29.—*Zercoseius spathuliger* (Leonardi), female. 28. Dorsum ; 29. Venter.

The venter of the female is well-sclerotised and the sternal shield bears the usual three pairs of setae. The metasternals are situated on platelets and the wedge-shaped genital shield is provided with a pair of simple setae. The ventri-anal shield occupies almost the entire region behind the genital shield. It carries seven pairs of setae excluding the three setae usually associated with the anus. The peritrematal shield is broad and fused with the dorsal shield in the scapular region ; the peritreme extends to coxa I.

The gnathosoma is normal for the subfamily. The digits of the chelicera are tridentate.

All legs terminate in ambulacra.

ZERCOSEIUS SPATHULIGER (Leonardi)

Scius spathuliger Leonardi, G. (1899) in Canestrini, G. Prosp. Acarof. Ital. **8** : 923, figs.
Ameroseius zerconiformis Berlese, A. (1905). Redia **2** : 234.

This small species (about 400 μ in length) is not uncommon in moss and humus under deciduous stands in Britain. The above account of the species and the figures will suffice for its identification.

Genus *PROCTOLAELAPS* Berlese s. lat.

Proctolaelaps Berlese, A. (1923), Redia **15** : 255.
Seiopsis Berlese, A. (1923). Redia **15** : 255 *syn. nov.*
Jordensia Oudemans, A. (1936). K.H.O.A., **3A** : 214 *syn. nov.*
Chamolaelaps Hull in Turk & Turk, S. (1952). Ann. Mag. nat. Hist. (12), **5** : 482 *syn. nov.*
Blattilaelaps Womersley, H. (1956). J. Linn. Soc. Lond. **42** : 566 *syn. nov.*

I have included in this genus those members of the *Melichares*-group which have nineteen or more setae on the " posterior dorsal shield " as the result of the occurrence of four or more parts of marginal setae on the lateral margins of the shield (Fig. 33). The genus may be readily separated into two groups, to which I have given subgeneric rank, on the basis of the degree of fusion of the peritrematal shield with the exopodal shield and the sclerotisation of the anal region.

In the subgenus *Proctolaelaps*, the peritrematal shield is free posteriorly although it may abut the exopodal shield in region of coxa IV and the female has an anal shield bearing the normal three setae. The majority of the known species also have the anal opening greatly enlarged as Berlese (1923) mentioned in his generic diagnosis. The sternal and wedge-shaped genital shield are of the usual form encountered in the subfamily and respectively bear six and two simple setae. The gnathosoma usually has the corniculi straight, subparallel and widely separated but in *Proctolaelaps* (*P.*) *hypudaei* (Oudms.) the corniculi are sinuous with the rostral setae stout and spine-like (Fig. 34). The transverse rows of denticles in the ventral groove are conspicuous. The tectum is variable in form and may have its anterior margin minutely denticulate or produced into three strong processes. Two types of chelicera occur in the species I have examined differing in the dentition of the fixed digit. In the *hypudaei*-group the fixed digit has a row of closely-set teeth along its cutting edge and hyaline denticulate appendage (Fig. 38). The *cossi*-group, on the other hand, never has more than three or four teeth in this digit and there is no evidence of a hyaline appendage. All the legs are relatively slender and have well-developed pretarsi and ambulacra. There are no macrosetae on tarsus IV.

The subgenus *Neojordensia* has the same type of chaetotactic pattern of the " posterior dorsal shield " as *Proctolaelaps* but differs in having the peritrematal shield fused with the exopodal shield posteriorly and in the increased sclerotisation of the anal region of the female. Except for the chaetotaxy of the dorsal shield, species of *Neojordensia* closely resemble those of the genus *Lasioseius*. The gnathosoma is essentially the same as in *Proctolaelaps*. The fixed digit of the chelicera has a row of small teeth.

Subgenus *PROCTOLAELAPS* Berlese

Type : *Proctolaelaps productus* Berlese, 1923.
The following six species are known from Europe :

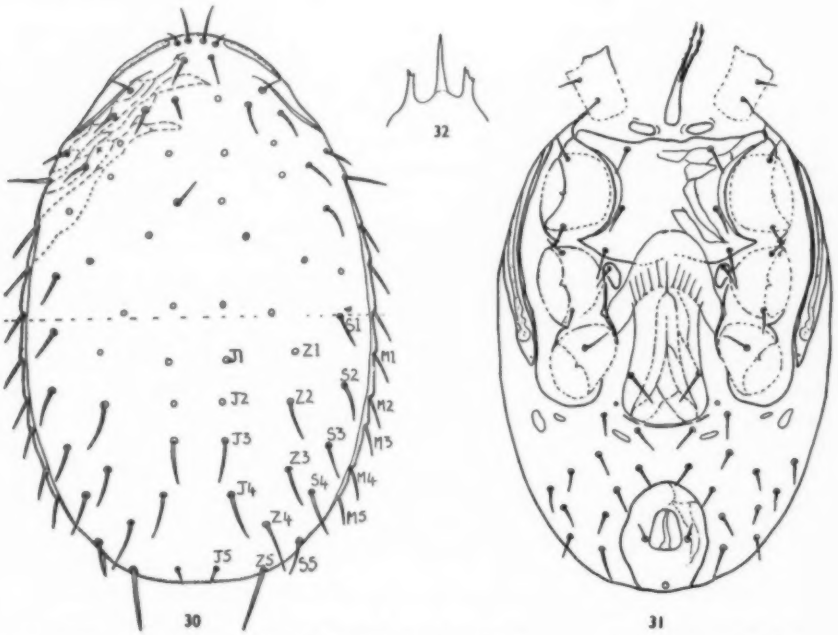
Key to females of the European species of the genus Proctolaelaps *Berl.* s. str.

1. Fixed digit of the chelicera with a row of closely-set teeth along its entire margin ..... 2.

–. Fixed digit of the chelicera with, at the most, three or four well-spaced teeth	4.
2. Rostral setae stout, spine-like ; corniculi sinuous (Fig. 34)	*P. hypudaei* (Oudemans).
–. Rostral setae simple ; corniculi normal	3.
3. Tectum with three well-developed processes ; setae of the Z series longer than the distance between their bases ..	*P. hystrix* (Vitzthum)
–. Tectum with its anterior margin minutely denticulate ; setae of the Z series shorter than the distance between their bases	*P. scolyti* sp. n.
4. Dorsal setae short ; seta J1 less than one-half the length of distance between the bases of J1 and J2	5.
–. Dorsal setae longer ; seta J1 longer than half the distance between the bases of J1 and J2	6.
5. With four small strongly sclerotised pre-endopodal shields (Fig. 40) ; endopodal shields in the region of coxae III and IV, large and conspicuous	*P. robustus* sp. n.
–. Without such pre-endopodal shields ; endopodal shields in the region of coxae III and IV, weak, inconspicuous	*P. eccoptogasteris* (Vitzthum).
6. Tectum with three strong processes ; with platelets between the genital and anal shields (Fig. 31)	*P. cossi* (Dugès)
–. Tectum with anterior margin denticulate ; without platelets between genital and anal shields	*P. pomorum* (Oudemans).

PROCTOLAELAPS (*P.*) *COSSI* (Dugès)

Gamasus cossi Dugès, A. (1834). Ann. Sci. nat. Paris s. 2, **1** : 19 ; Oudemans, A. C. (1936). K.H.O.A. Leiden : 214.



Figs. 30–32.—*Proctolaelaps* (*P.*) *cossi* (Dugès), female. 30. Dorsum ; 31. Venter ; 32. Tectum.

Female. Strongly sclerotised species with the dorsal shield (560 × 360 μ) bearing forty-three pairs of simple setae distributed as in Fig. 30. " Posterior dorsal shield " with twenty pairs of setae. Setae J3 (33 μ) longer than one-half the distance between the bases of J3 and J4 (38 μ). Dorsal shield reticulated.

Sternal shield with three pairs of setae ; metasternal shields well-developed, free (Fig. 31). Pre-endopodal shields strongly sclerotised. Genital shield wedge-shaped with the usual pair of setae. Anal shield with anal opening large. Integument posterior to coxae IV with twenty-four setae. Platelets present between genital and anal shields. Metapodalia as figured ; exopodal shield entire ; peritrematal shield free posteriorly.

Gnathosoma normal for the genus. Corniculi strong ; rostral setae long and simple. Ventral groove with six transverse rows of denticles. Tectum produced into three strong processes (Fig. 32). Chelicera simple ; fixed digit with three well-spaced teeth.

All legs with pretarsi and ambulacra. Tarsi IV slightly curved.

Distribution. The above redescription of the species is based on a single specimen collected from the larva of *Cossus cossus* Linn. at Zevenhuizen, Netherlands. The original description of this species was given by Lyonet (1760) who did not name the mite. His material was also collected off *cossus* in the Netherlands.

PROCTOLAELAPS (*P.*) *HYPUDAEI* (Oudemans)

Hypoaspis hypudaei Oudemans, A. C. (1902). Tijdschr. Ent. **45** : 21, figs. ; Oudemans, A. C. (1914). Arch. Naturgesch. **79A** (8) : 185, figs.

Lasioseius (L.) *innumerabilis* Berlese, A. (1918). Redia **13** : 132 *syn. nov.*

Typholodromus bulbicolus Oudemans, A. C. (1929). Ent. Ber. Amst. **8** : 15 ; Oudemans, A. C. (1929). tom. cit.: 29.

Garmania bulbicola, Nesbitt, H. H. J. (1951). Zool. Verhandl. Leiden No. 12 : 46, figs.

Lasioseius alpinus Schweizer, J. (1949). Rés. Rech. scient. Parc Nation. Suisse **2** : 46, fig. *syn. nov.*

Lasioseius ventritrichosus Schweizer, J. (1949). tom. cit.: 47, fig. *syn. nov.*

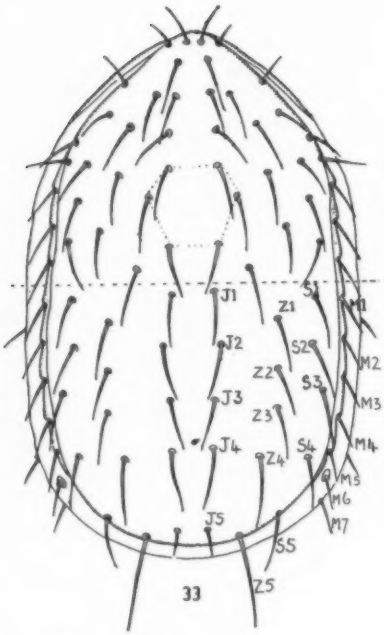
Garmania hypudaei, Evans, G. O. (1954). Proc. zool. Soc. Lond. **123** : 794.

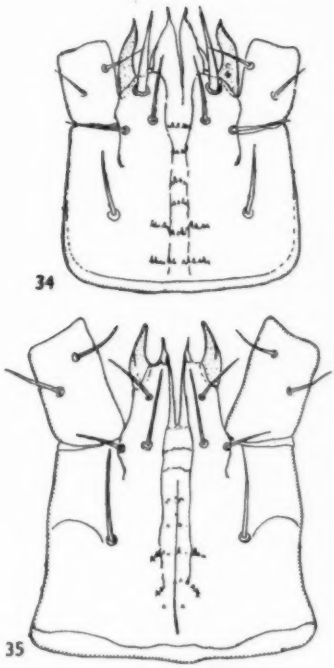
Jordensia hypudaei, Evans, G. O. (1957). J. Linn. Soc. Lond. (Zool.) **42** : 227.

Female. The descriptions and figures of this species given by Oudemans (1902 and 1914) and Nesbitt (1951) are adequate for its identification. The characteristic feature of *hypudaei* is the presence, in both sexes, of stout, spine-like rostral setae and sinuous corniculi (Fig. 34). The dorsal shield bears forty-three pairs of relatively long simple setae distributed as in Fig. 33. The tectum has a denticulate anterior margin and the fixed digit of the chelicera has a row of closely-set teeth along its cutting edge.

It is possible that *Lasioseius fissuratus* Berl., 1916 is also a synonym of *hypudaei*.

Distribution. This is a widely distributed species in a variety of terrestrial habitats. It has been recorded from the nests of small mammals, feeding (?) on tyroglyphids in stored food products and in decaying vegetation in the soil. I have seen material from Europe, S. Africa, N. America, Indonesia, Australia and New Zealand.





Figs. 33–34.—*Proctolaelaps* (*P.*) *hypudaei* (Oudemans), female. 33. Dorsum ; 34. Venter of gnathosoma.

Fig. 35.—*Proctolaelaps* (*P.*) *pomorum* (Oudemans), female. Venter of gnathosoma.

PROCTOLAELAPS (*P.*) *POMORUM* (Oudemans)

Typhlodromus pomorum Oudemans, A. C. (1929). Ent. Ber. Amst. **8** (170) : 31.
Garmania pomorum, Nesbitt. H. H. J. (1951). Zool. Verhandl. No. 12 : 48, figs.
Evans, G. O. (1954). Proc. zool. Soc. Lond. **123** : 794, figs.

Female, This sex has been adequately described and figured by Nesbitt (1951). The chaetotactic pattern on the dorsal shield is essentially the same as in *hypudaei*. The setae are somewhat shorter and thicker in their basal halves than in *hypudaei*. The corniculi and rostral setae are normal (Fig. 35) and the fixed digit of the chelicera is provided with two blunt teeth. The tectum has its anterior margin denticulate.

Male. This sex has been described and figured by Evans (1954).

Distribution. Oudemans collected this species on an apple in Arnhem, Netherlands. It has subsequently been recorded from stored foodstuffs infested with tyroglyphid mites in a dwelling house in Lancashire.

PROCTOLAELAPS (*P.*) *HYSTRIX* (Vitzthum)

Lasioseius (*Lasioseius*) *hystrix* Vitzthum, H. G. (1923). Arch. Naturgesch. **89A** (2) : 105, figs.

Female. Dorsal shield (approx. 440 × 265 μ) with forty-two pairs of simple setae of which twenty-three pairs are situated on the " anterior dorsal shield ". Setae long, those of the J (J1–J4, 57–66 μ) and Z series longer than the distance between their bases. Only four pairs of marginal setae on the " posterior dorsal shield ". Surface of shield reticulated.

The sternal and genital shields are completely reticulated. The anal shield is normal for the genus. The pre-endopodal shields are weakly sclerotised. The metasternal shields are free. The anal shield has a very large anal opening. The integument posterior to coxae IV has about twenty-four simple setae. The metapodal shields are conspicuous.

The venter of the gnathosoma is typical of the genus with the rostral setae simple and the corniculi pointed distally. Anterior margin of the tectum produced into three strong subequal processes as in certain species of *Leioseius* and *Arctoseius*. The fixed digit of the chelicera has a row of small closely-set teeth along its cutting edge.

All legs have well-developed pretarsi and ambulacra.

Distribution. The above redescription of the species is based on the type series (No. 2372 in the Vitzthum Collection at München). The species has been recorded from *Dendroctonus micans* Kug. and *Hylastes ater* Payk.—(Vitzthum, 1923)—in Germany. The record of this species from *Ips typographus* by Hirschmann & Rühm (1954) is based on a misidentification.

PROCTOLAELAPS (*P.*) *ECCOPTOGASTERIS* (Vitzthum)

Lasioseius (*Lasioseius*) *eccoptogasteris* Vitzthum, H. G. (1923). Arch. Naturgesch. **89A** (2) : 108, figs.

Female. Dorsal shield (approx. 450 × 240 μ) with forty-two pairs of setae as in the preceding species ; " anterior dorsal shield " with twenty-three pairs. Dorsal setae, with the exception of the verticals and Z5, short ; those of the J series (J1–J4, 15–17 μ) less than one-half the length of the distance between their bases. Z5 (approx. 45 μ) considerably longer than the other dorsal setae. Surface of shield reticulated.

Sternal, metasternal, genital and anal shields typical of the genus. Anal opening large. Pre-endopodal shields weakly sclerotised, elongate ; metapodal shields (two on each side of the opisthosoma) with the posterior member considerably longer than broad.

Gnathosoma normal ; rostral setae simple, corniculi long and slender. Tectum with rounded anterior margin minutely denticulate. Fixed digit of the chelicera with two or three well-spaced teeth.

All legs with pretarsi and ambulacra.

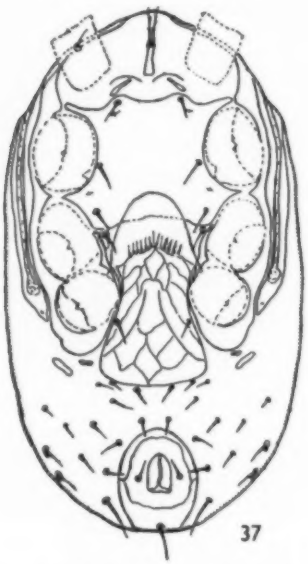
Distribution. The above redescription of the species is based on the type series (No. 2369 in the Vitzthum Collection at München). *P. eccoptogasteris* is known only from *Eccoptogaster laevis* Chap. in Germany.

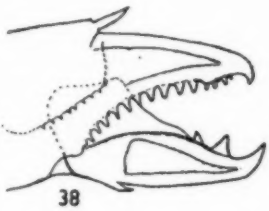
PROCTOLAELAPS (P.) SCOLYTI, sp. n.

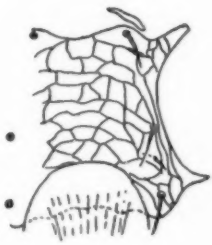
Female. Dorsal shield (approx. 420 × 320 μ) reticulated and bearing forty-two pairs of simple setae of which twenty-three pairs occur on the

" anterior dorsal shield ". Setae relatively long as in *hypudaei* ; J1–J4 ranging from 36 to 40 μ. Z5 measures about 53 μ.

Sternal shield ornamented as in Fig. 36 ; sternal setae normal. Pre-endopodal shields elongate. Genital shield wedge-shaped and with a pair of setae (Fig. 37). Anal shield with anal opening enlarged. Interscutal membrane posterior to coxae IV with twelve pairs of setae (excluding members of the marginal series). Metapodalia weakly sclerotised. Endopodal shields entire ; peritrematal shields free posteriorly.







Figs. 36–38.—*Proctolaelaps* (*P.*) *scolyti* sp. n., female. 36. Sternal shield ; 37. Venter ; 38. Chelicera.

Gnathosoma normal ; corniculi straight, rostral setae only slightly enlarged. Tectum with rounded anterior margin denticulate. Fixed digit of the chelicera multidentate ; movable digit bidentate (Fig. 38). Denticulate hyaline process present as in *hypudaei*.

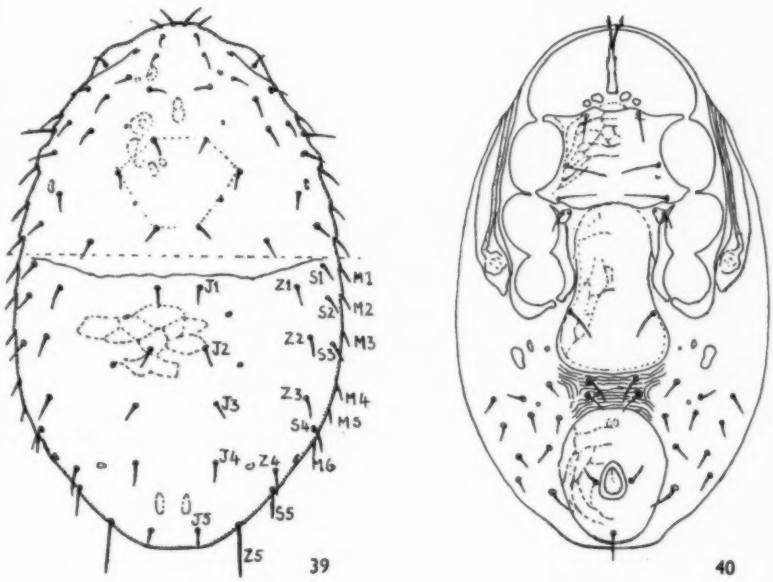
All legs with pretarsi and ambulacra.

Distribution. Four females from *Scolytus* sp. collected at Oxford, England (Holotype ; 1957 : 11 : 22 : 17 ; paratypes 1957 : 11 : 22 : 18–20) and a single female on a chateid, *Entodon* sp., England (precise locality not available) ; 1957 : 11 : 22 : 21.

This species superficially resembles *hypudaei* but may be readily distinguished from it by the structure of the gnathosoma and the ornamentation of the sternal and genital shields. In *hypudaei* the sternal shield is only weakly ornamented along its lateral margins—the remainder of the shield is smooth—and the genital shield has only an inverted V-shaped figure.

PROCTOLAELAPS (P.) ROBUSTUS, sp. n.

Female. A strongly sclerotised species. Dorsal shield (approx. 385 × 250 μ) reticulated and bearing forty-four pairs of simple setae distributed as in Fig. 39. Setae short ; J1–J4 ranging from 15 to 19 μ in length. Z5 (37 μ) considerably longer than the other setae on the shield.



Figs. 39–40.—*Proctolaelaps* (*P.*) *robustus* sp. n., female. 39. Dorsum ; 40. Venter.

Sternal, metasternal, genital and anal shields of the type usually encountered in the genus (Fig. 40). Four small pre-endopodal shields conspicuous, endopodal shields in the region of coxae III and IV strongly developed. Anal opening not markedly enlarged. Integument posterior to coxae IV with twelve pairs of simple setae ; metapodal shields well developed. Exopodal shields entire ; peritrematal shields free posteriorly. Peritremes extending beyond coxae I.

Gnathosoma normal ; rostral setae simple, corniculi long and slender. Tectum with its anterior margin minutely denticulate. Fixed digit of the chelicera with two ill-defined teeth in the distal third of the digit ; movable digit unidentate.

All legs with pretarsi and ambulacra.

Locality. Two females (Holotype : 1957 : 11 : 22 : 56 ; paratype : 1957 : 11 : 22 : 57) in moss in pine forest, Trossachs, Perthshire, Scotland (Coll. K. H. Hyatt).

Subgenus *NEOJORDENSIA* Evans

Neojordensia Evans, G. O. (1957). J. Linn. Soc. Lond. Zool. **43** : 2.

Type : *Seiulus levis* Oudemans & Voigts, 1904.

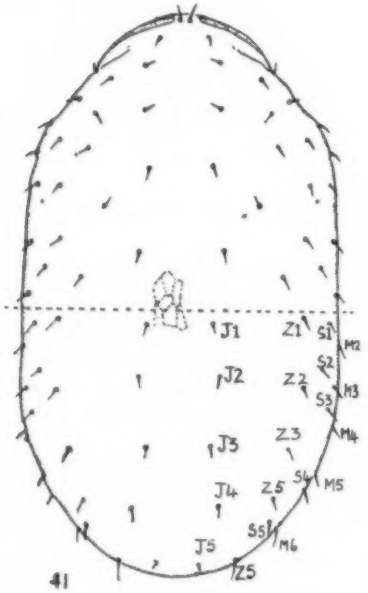
At present this subgenus contains only two species both of which occur in Britain. They may be distinguished as follows :

1. With jugularia (Fig. 42) ; exopodal shields fragmented ; ventri-anal shield in the female with only four pairs of preanals ; paravertical setae absent ..... *P. (N.) levis* Oudemans & Voigts
–. Without jugularia (Fig. 44) ; exopodal shield entire ; ventri-anal shield in the female with six pairs of preanals ; paravertical setae present ..... *P. (N.) lawrencei* sp. n.

PROCTOLAELAPS (*NEOJORDENSIA*) *LEVIS* (Oudemans & Voigts)

Seiulus levis Oudemans & Voigts in Voigts, H. & Oudemans, A. C. (1904). Zool. Anz. **12** : 654 ; Voigts, H. & Oudemans, A. C. (1905). Abh. Nat. Ver. Bremen **18** : 232, figs. ; Halbert, J. N. (1915). Proc. Roy. Irish Acad. **39** (ii) : 76, fig.

Female. Dorsal shield (460 × 290 μ) finely reticulated with forty-two pairs of short simple setae (Fig. 41). " Posterior dorsal shield " with twenty pairs of setae of which five pairs belong to the marginal series. Paravertical setae absent.



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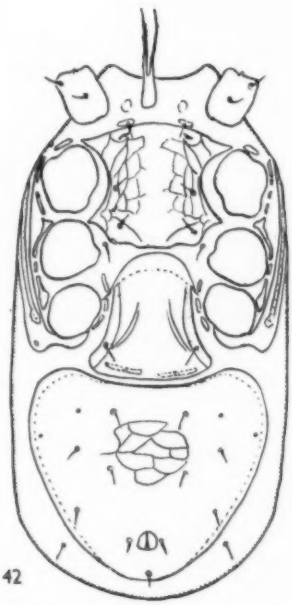

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Figs. 41–42.—*Proctolaelaps* (*Neojordensia*) *levis* (Oudemans & Voigts), female. 41. Dorsum. 42. Venter.

Jugular shields small ; sternal shield with two pairs of setae (Fig. 42). Metasternal setae on the integument. Endopodal shields weakly developed in the region of coxae III and IV. Genital shield normal and with four platelets posteriorly. Ventri-anal shield (165 × 210 μ), anterior margin concave, with four pairs of preanals. Metapodalia absent. Peritrematal shield fused with the exopodal shield posterior to coxae IV ; exopodal shields fragmented.

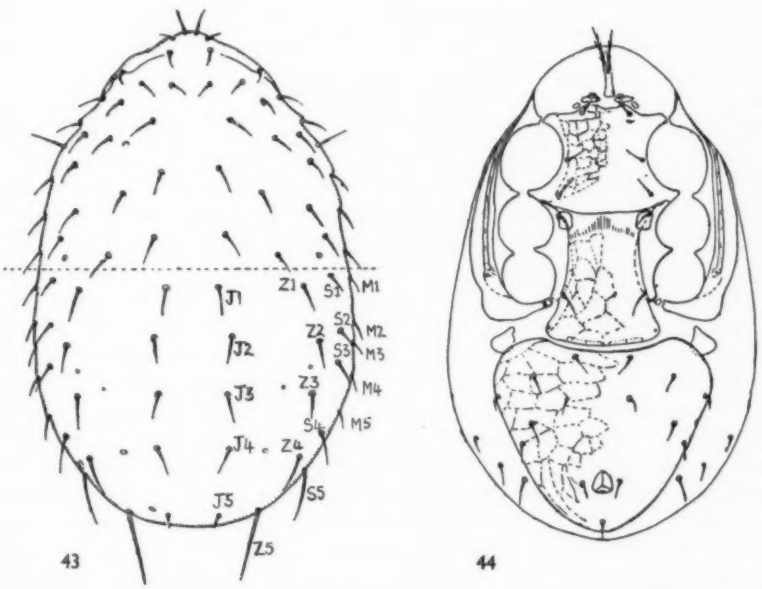
Gnathosoma normal. Tectum with a smooth or very minutely denticulate anterior margin. Fixed digit of the chelicera with six teeth ; movable digit bidentate.

All legs with pretarsi and ambulacra.

Distribution. This species has been recorded from Germany (Voigts & Oudemans, 1904), Austria (Franz, 1954) and Ireland (Halbert, 1915). I have examined specimens from : sphagnum, Cockhill, Yorkshire (coll : J. T. Salmon, 1951) ; in decaying vegetation, County Cork, Ireland (coll : T. Clay, 1953) ; in flood debris, Rydal Water, Westmorland (coll : M. E. Bacchus, 1954) and at roots of rushes, St. Agnes, Isles of Scilly, Cornwall (coll. K. H. Hyatt, 1957).

PROCTOLAELAPS (NEOJORDENSIA) LAWRENCEI, sp. n.

Female. Dorsal shield (410 × 275 μ) finely reticulated and bearing forty-three pairs of simple setae (Fig. 43). " Posterior dorsal shield " with twenty pairs of setae of which five pairs belong to the marginal series. Z5, longest seta of the dorsum, is about 55 μ in length.



Figs. 43–44.—*Proctolaelaps* (*Neojordensia*) *lawrencei* sp. n., female. 43. Dorsum. 44. Venter.

Three pairs of small pre-endopodal shields are conspicuous (Fig. 44). The reticulated sternal shield bears three pairs of simple setae ; the metasternal shields are free. Endopodal shields in the region of coxae III and IV strongly sclerotised. Genital shield normal, the four platelets posterior to the shield fused into a sclerotised strip. Anterior margin of the ventrianal shield (143 × 187 μ) concave ; peritrematal shield fused posteriorly with the exopodal shield.

Gnathosoma with corniculi parallel ; rostral setae simple. Tectum trispinate, median process broadly triangular and extending beyond the apex of the lateral processes. Fixed digit of the chelicera with a row of small closely-set teeth.

All legs with pretarsi and ambulacra.

Locality. Two females (Holotype : 1957 : 11 : 22 : 48 ; paratype : 1957 : 11 : 22 : 49) from moss on trunk of tree, Forest of Dean, Gloucestershire. (Coll. J. T. Salmon).

The species is named after Mr P. N. Lawrence, Department of Entomology, British Museum (Natural History) whose extensive collecting of soil Acarina during the last four years has greatly enriched the Museum Collections.

Genus *MELICHARES* Hering s. lat.

Melichares Hering, E. (1838). Acta. Acad. Caes. Leop. Car. Nat. Cur. **18** : 626.
Garmania Nesbitt, H. H. J. (1951). Zool. Verh. Leiden No. 12 : 43 syn. nov.
Paragarmania Nesbitt, H. H. J. (1951). . . . ibid. . . . : 49 syn. nov.

Although Hering's original description of the type species of the genus, *Melichares agilis* Hering, contains many inaccuracies, there can be little doubt that the species redescribed under that name by Oudemans (1905) is conspecific with *agilis*. Unfortunately, Oudemans in 1929 described the same species under *Typhlodromus domestica* and this name has been widely used for species since Nesbitt (1951) made it the type of the genus *Garmania*.

The known species of *Melichares* are weakly sclerotised and active. In the adult stages, the dorsal shield is entire although it may be strongly incised in the deutonymph. The " posterior dorsal shield " bears fifteen pairs of setae ; the marginals are never fused with the shield. The chaetotaxy of the " anterior dorsal shield " is not constant, for example, depending on the number of marginal setae situated on the shield, the number varies from fourteen pairs in *agilis* to twenty-one pairs in *Melichares* (*Blattisocius*) *dentriticus* (Berlese). Only in *agilis* do we find setae on the anterior third of the peritrematal shield.

The venter of the female has a well-developed sternal shield bearing two or three pairs of setae. The genital shield is usually wedge-shaped and always carries the genital setae. The degree of sclerotisation of the anal region varies considerably ; *agilis* having an anal shield whereas all other known species have a ventri-anal shield. The peritrematal shield may or may not be fused with the exopodal shield in the region or coxae IV. The peritreme is sometimes strongly reduced in length.

The gnathosoma differs considerably from that described for other genera of the Aceosejinae in that the corniculi are long, slender and convergent (Fig. 4). In this feature, the species resemble most closely members of the genus *Typhlodromus* (Phytoseiidae). Further, there is a tendency for a reduction in the number of transverse rows of denticles in the ventral grooves. The fixed digit of the chelicera is never multidentate as in *Lasioseius* and in some species it may be reduced in length. The movable digit is always normal and may be uni-or tridentate. The chaetotaxy of the pedipalp is normal.

All legs are provided with pretarsi and ambulacri. Tarsus IV in some species has a macroseta.

I have subdivided the genus *Melichares* into two subgenera on the basis of the sclerotisation of the venter of the female. In *Melichares* s. str. the female has an anal shield and the peritrematal shield is not (or weakly) fused with the exopodal shield in the region of coxa IV. The other subgenus, *Blattisocius* Keegan, is characterised by having a ventri-anal shield in the female and the peritrematal shield strongly fused with the exopodal shield in the female and the peritrematal shield strongly fused with the exopodal shield in the region of coxa IV. I do not consider the modifications of the chelicerae and peritreme in the females of certain species of *Blattisocius* to warrant a further division of this subgenus. I have therefore considered *Paragarmania* Nesbitt to be a synonym of *Melichares* s. lat.

Subgenus *MELICHARES* Hering s. str.

Type : *Melichares agilis* Hering, 1838.

At present this subgenus is represented by the type species only.

MELICHARES (*MELICHARES*) *AGILIS* Hering

Melichares agilis Hering, E. (1839). Acta. Acad. Caes. Leop. Car. Nat. Cur. **18** : 620, figs. ; Oudemans, A. C. (1905). Tijdschr. Ent. **48** : 236, figs.

Typhlodromus domesticus Oudemans, A. C. (1929 a). Ent. Ber. Amst. **8** : 29 ; Oudemans, A. C. (1930). Ent. Ber. Amst. **8** : 49 *syn. nov.*

Garmania domestica, Nesbitt, H. H. J. (1951). Zool. Verh. Leiden No. 12 : 44 figs.

Female. Dorsal shield entire (approx. 460 × 210 μ) with twenty-nine pairs of simple setae distributed as in Fig. 45. " Anterior dorsal shield " with fourteen pairs of relatively short setae. Longest setae on the dorsum are Z5 which measure about 56 μ in length. Lateral interscutal membrane in the region of the " anterior dorsal shield " with seven pairs of setae. Anterior region of the peritrematal shield with two setae.

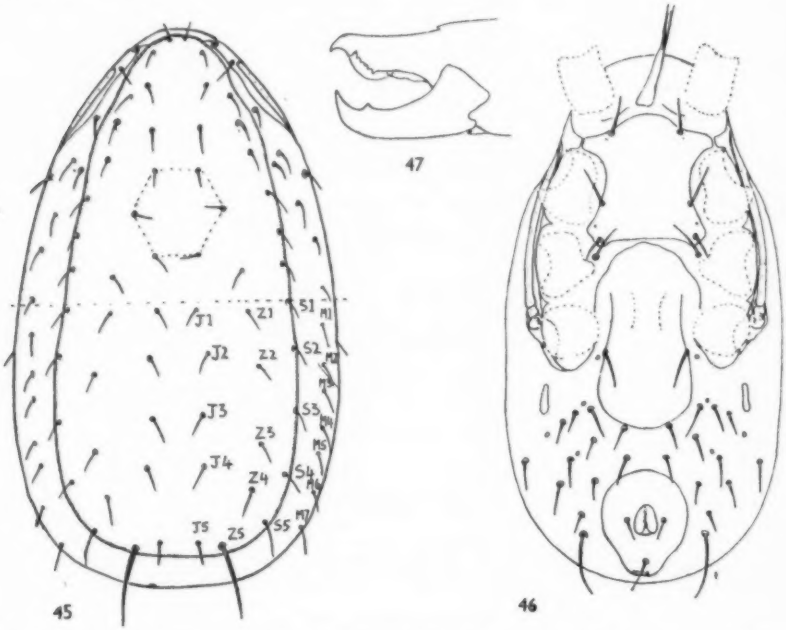
Sternal shield with three pairs of setae ; metasternals on the integument (Fig. 46). Genital shield large, slightly convex posteriorly. Anal shield subcircular with the usual three setae. Stigma in the region of coxa IV. Peritreme reaching to about the level of the posterior margin of coxa I.

Gnathosoma with the corniculi slender and convergent (Fig. 4). Tectum with its anterior margin smooth. Fixed digit of the chelicera with four or five small teeth in its distal half ; movable digit unidentate (Fig. 47).

All legs slender with pretarsi and ambulacra. No macrosetae on tarsus IV.

Male. Chaetotaxy of the dorsal shield (415 × 187 μ) and lateral interscutal membrane essentially the same as in the female.

Sterniti-genital shield with five pairs of setae. Ventri-anal shield (156 × 170 μ) free and with seven pairs of preanals. Peritreme and peritrematal shield as in the female.



Figs. 45–47.—*Melichares* (*M.*) *agilis* Hering, female. 45. Dorsum ; 46. Venter ; 47. Chelicera.

Gnathosoma with the corniculi not as strongly convergent as in the female. Fixed digit of the chelicera with six or seven small teeth along its cutting edge ; movable digit unidentate. Spermatophoral process simple.

Distribution. This species is commonly found associated with tyroglyphid mites in dried fruit (the habitat given by Hering, 1838). It has been recorded from Germany (Hering ; Oudemans, 1905 and 1929) and Britain (Evans, 1954).

Subgenus *BLATTISOCIUS* Keegan

Blattisocius Keegan, H. L. (1944). J. Parasit. **30** : 181.

Type : *Blattisocius triodons* Keegan, 1944 (= *Lasioseius tarsalis* Berl.).

Key to females of the British species of Blattisocius *Keegan*

1. Peritreme reduced, not extending beyond coxa II (Fig. 48) ; fixed digit of the chelicera considerably shorter than the movable digit (Figs. 49)..... 2.
–. Peritreme normal, extending to coxa I ; both digits of the chelicera equally well developed (Fig. 55)..... 3.

2. Peritreme reaching to about the posterior margin of coxa II (Fig. 48) ; fixed digit of the chelicera very short, without teeth, pilus dentilis very long (Fig. 49) ..... *M.* (*B.*) *tarsalis* (Berl.).

-. Peritreme very short, not reaching the middle of coxa III (Fig. 52) ; fixed digit of the chelicera with minute teeth and about two-thirds the length of the movable digit (Fig. 53) ..... *M.* (*B.*) *keegani* Fox.

3. Tarsus IV with a long whip-like macroseta (Fig. 56) ; sternal setae III and IV on a platelet connected to the sternal shield by the endopodal shield ..... *M.* (*B.*) *dentriticus* (Berl.).

-. Tarsus IV without macroseta ; metasternal shields free, sternal shield with three pairs of setae ..... *M.* (*B.*) *pomorum* (Oudms.).

MELICHARES (*BLATTISOCIUS*) *TARSALIS* (Berlese)

Lasioseius (*L.*) *tarsalis* Berlese, A. (1918). Redia **13** : 134.
Typhlodromus tincivorus Oudemans, A. C. (1929 a). Ent. Ber. Amst. **8** (170) : 34 *syn. nov.*
Blattisocius triodons Keegan, H. L. (1944). J. Parasit. **30** : 181, figs.
Typhlodromus tineivorans, Hughes, A. M. (1948). Mites associated with stored food products, H.M.S.O. Lond. : 144, figs.
Lasioseius similis Schweizer, J. (1949). Rés. Rech. scient. Parc Nation. Suisse **2** (N.S.) : 49, fig. *syn. nov.*
Blattisocius tineivorus, Nesbitt, H. H. J. (1951). Zool. Verh. Leiden No. 12 : 51 figs.

Female. Weakly sclerotised species. Dorsal shield (approx. 480 × 250 μ) faintly reticulated and bearing thirty-three pairs of simple setae of which fifteen pairs are situated on the " posterior dorsal shield ". There are five pairs of marginal setae situated on the integument lateral to the " anterior dorsal shield ". Seta J2 lies well outside the line connecting the bases of J1 and J3.

The sternal shield carries three pairs of setae ; setae II and III lie on the margin of the shield. The metasternal setae are situated on the integument. Genital shield wedge-shaped with a pair of setae. Ventri-anal shield long and relatively narrow, and bearing three pairs of preanals. Peritreme short, reaching to about the level of the posterior margin of coxa II (Fig. 48).

Gnathosoma with the corniculi slender and convergent ; rostral setae simple. Tectum with anterior margin smooth. Fixed digit of the chelicera markedly reduced, without teeth ; pilus dentilis long, setiform (Fig. 49). Movable digit tridentate.

All legs with pretarsi and ambulacra. No macrosetae on tarsus IV.

Male. This sex has been described by Oudemans (1929) and figured in Nesbitt (1951). The form of the dorsal shield and the peritreme are essentially the same as in the female. The fixed digit of the chelicera is not markedly reduced in length.

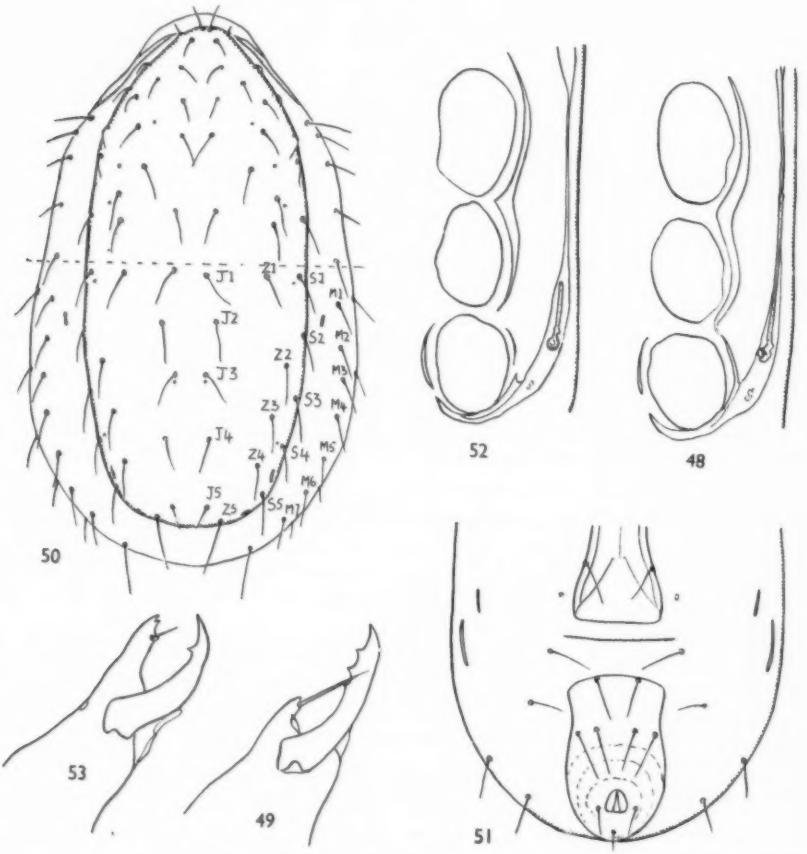
Distribution. The type locality is given as " *in detritus foeni, in presepibus, Florentiae* ". This species has also been recorded from U.S.A., Britain and Switzerland. It is usually associated with insect pests in stored food products and in experimental cultures.

MELICHARES (*BLATTISOCIUS*) *KEEGANI* Fox

Blattisocius keegani Fox, I. (1947). Ann. ent Soc. Amer. **40** : 599, figs. ; Cunliffe, F. & Baker, E. W. (1953). Pinellas Biol. Lab. Pub. No. 1 : 7, figs.

Female. Weakly sclerotised species. Dorsal shield with thirty-three pairs of simple setae distributed as in Fig. 50. Setation of the lateral interscutal membrane as in *tarsalis*.

Chaetotaxy and form of the sternal and genital shields and the ventri-anal shield as in *tarsalis* (Fig. 51). Peritrematal shield fused with the exopodal shield in the region of coxa IV ; peritreme very short, extending to about the middle of coxa III (Fig. 52).



Figs. 48–49.—*Melichares* (*Blattisocius*) *tarsalis* (Berlese), female. 48. Peritreme ; 49. Chelicera.
Figs. 50–53.—*Melichares* (*Blattisocius*) *keegani* Fox, female. 50. Dorsum ; 51. Anal region ; 52. Peritreme ; 53. Chelicera.

Gnathosoma with corniculi convergent. Fixed digit of the chelicera dentate but shorter than the movable which is unidentate (Fig. 53).

All legs with pretarsi and ambulacra. Leg IV without macrosetae.

Distribution. This species was first collected by Fox (1947) from *Rattus norvegicus* at San Juan, Puerto Rico. It has subsequently been found to be

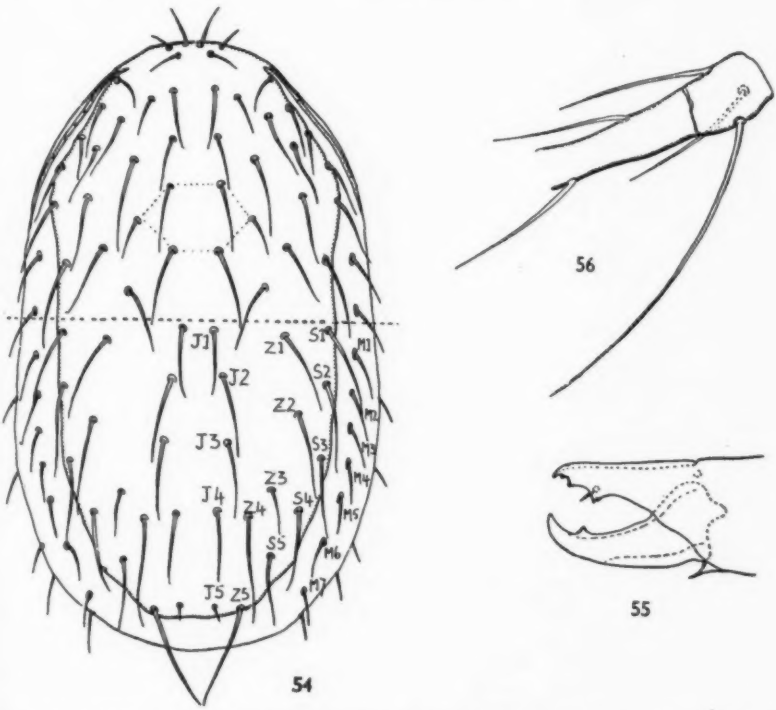
common in insect cultures and in stored food products infested with various insects. The Collection of the British Museum (Natural History) contains specimens collected on *Phorium tenax* Forst at Pahang, Malaya. In the latter locality the species was associated with tetranychids.

MELICHARES (*BLATTISOCIUS*) *DENTRITICUS* (Berlese)

Lasioseius (*L.*) *dentriticus* Berlese, A. (1918). Redia **13** : 133.
Lasioseius fimbriatus Halbert, J. N. (1923). J. Linn. Soc. Lond. (Zool.) **35** : 368, fig. *syn. nov.*
Sciulus amboinensis Oudemans, A. C. (1925). Ent. Ber. Amst. **7** (146) : 30 *syn. nov.*
Garmania (*Paragarmania*) *amboinensis*, Nesbitt, H. H. J. (1951). Zool. Verh. Leiden No. 12 : 50, figs. ; Evans, G. O. (1954). Proc. zool. Soc. Lond. **123** : 796, figs.

Female. Dorsal shield faintly reticulated and bearing thirty-six pairs of setae distributed as in Fig. 54. " Posterior dorsal shield " with fifteen pairs of setae. J1–J4 longer than the distance between their bases. Marginal series free.

Anterior third of sternal shield ornamented ; sternal shield with only two pairs of setae. Setae III and IV on a large plate connected to the sternal shield by the endopodal shield. Genital shield wedge-shaped but constricted



Figs. 54–56.—*Melichares* (*Blattisocius*) *dentriticus* (Berlese), female. 54. Dorsum ; 55, Chelicera ; 56. Basal half of tarsus IV.

between coxae IV. Ventri-anal shield with four pairs of preanal setae. Metapodals elongate. Peritrematal shield fused with the exopodal shield in the region of coxa IV. Peritreme reaching to about the middle of coxa I.

Gnathosoma with corniculi slender and convergent ; rostral setae simple. Tectum with its anterior margin smooth and rounded. The fixed digit of the chelicera with three or four small teeth restricted to the distal third of the digit ; movable digit unidentate (Fig. 55).

All legs with pretarsi and ambulacra. "Metatarsus" IV with a macroseta (Fig. 56).

Distribution. Berlese records this species "in nidis Columbarum", Florence. Halbert (1923) found it on sprouting potatoes, Dublin : Oudemans (1925) records it from a microchiropteron at Ambon, and Evans (1954) redescribes the species from material collected from the thorax of *Caradrina morpheus*, Darlington, Yorkshire.

MELICHARES (*BLATTISOCIUS*) *MALI* (Oudemans)

Typhlodromus mali Oudemans, A. C. (1929 a). Ent. Ber. Amst. **8** (170) : 30.
Garmania (*Paragarmania*) *mali*, Nesbitt, H. H. J. (1951). Zool. Verh. Leiden No. 12 : 49, figs.

I have not examined specimens of this species which is adequately described and figured in Nesbitt (1951). The dorsal shield measures 518 × 310 μ. The unidentate fixed digit of the chelicera although not reduced in length has a long pilus dentilis as in *M.* (*B.*) *tarsalis*. The sternal shield of the female has three pairs of setae. There are no macrosetae on tarsus IV.

Distribution. Oudemans took the type specimens on the bark of *Pyrus malus* and in a hole in an apple at Amsterdam and Arnhem respectively. Turk & Turk (1952) record the species from dried currants (associated with tyroglyphids) at Kahenny, County Dublin, Eire.

Genus *IPHIDOZERCON* Berlese

Iphidozercon Berlese, A. (1903). Redia **1** : 246.
Arctosciopsis Evans, G. O. (1954). Proc. zool. Soc. Lond. **123** : 796.

Type : *Eviphis gibbus* Berlese, 1903.

There are strong affinities between this genus and *Arctoseius* especially in the chaetotaxy of the dorsal shield and the sclerotisation of the venter. The dorsal shield, however, is entire in the deutonymph and the adult, and bears thirty-two pairs of simple setae of which fourteen pairs are situated on the "posterior dorsal shield". The chaetotactic pattern of this region of the shield is essentially the same as in *Arctoseius*. In the adults of some species, the vertex is directed downwards so that the vertical setae are not visible when the mite is viewed from above. This only applies to the adult stages since in the deutonymphs the vertical setae are in their normal position. The dorsal shield covers the entire dorsum of the mite with the result that the marginal series of setae appear to be ventral in position.

The sternal shield in the female is narrow and not fused with the endopodal shields. It bears three pairs of setae. The metasternals are free. The form

of the genital shield is essentially the same as in the species of *Arctoseius* ; the genital setae lying off the shield. The anal shield carries the usual three setae although a ventri-anal shield of the type found in *A. magnanalis* may be present. In all the species I have examined, the peritrematal shield is strongly developed and the peritreme extends beyond coxa I.

The sclerotisation of the venter of the male is the same as in *Arctoseius*.

The gnathosoma is normal with the corniculi relatively short and stout, and widely separated distally. The tectum is trispinate and the chelicerae chelate-dentate with a simple spermatophoral process in the male. All legs terminate in ambulacra. Leg II of the male is unarmed.

There has been considerable confusion in the literature concerning the identity of the genus *Iphidozercon*. Most authors have considered *I. gibbus* to be congeneric with *Emeus inexpectatus* Oudemans, 1903 and have defined the genus on the basis of that species. It was not until recently that *gibbus* was " rediscovered " and its systematic position established (Evans, 1957).

The following three species keyed below occur in Britain. *Lasioseius* (*L.*) *venustulus* Berl., 1917 ; *Lasioseius* (*L.*) *pulvisculus* Berlese and *Lasioseius insularis* Willmann, 1952 must also be transferred to this genus. All have the *minutus*-type of vertex.

Key to females of the British species of Iphidozercon *Berlese*

1. Vertical setae visible from above ; dorsal shield with coarse punctures ..... *I. minutus* (Halbert).
—. Vertex directed downwards, vertical setae not visible from above (Fig. 57) ..... 2.
2. Dorsal shield with a prominent mid-dorsal elevation (Fig. 58) ; vertical setae short, spinose ..... *I. gibbus* (Berlese).
-. Dorsal shield without such elevation ; vertical setae longer, setiform ..... *I. corticalis* sp. n.

IPHIDOZERCON GIBBUS Berlese

Eviphis gibbus Berlese, A. (1903). Redia **1** : 246.

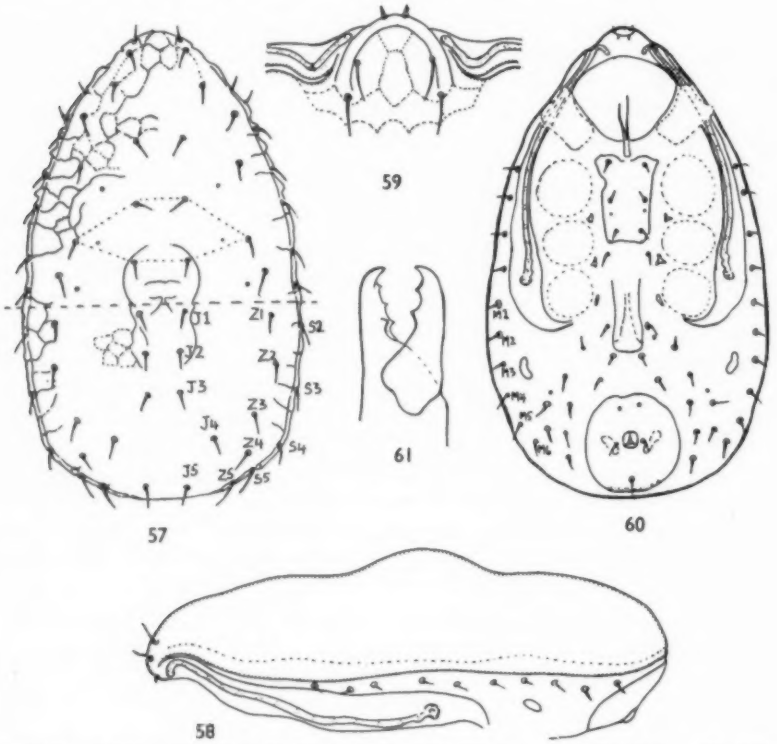
Female. Dorsal shield (approx. 460 × 300 μ) entire with thirty-two pairs of short simple setae distributed as in Fig. 57. Mid-dorsal region with a conspicuous elevation (Fig. 58). Vertex directed downwards so that vertical setae are not visible from above ; vertical setae short, spinose (Fig. 59). Marginal series ventral in position.

Sternal shield narrow, not fused with the endopodals, bearing three pairs of setae. Metasternal setae free. Genital shield long and narrow, without genital setae. Metapodal shields conspicuous (Fig. 60). Chaetotaxy of the region posterior to coxae IV as figured. Anal shield subcircular and with the usual three setae. Peritrematal shield strongly developed with the peritreme extending beyond coxa I.

Gnathosoma normal. Tectum trispinate. Movable digit of the chelicera bidentate ; fixed digit tri-or quadridentate (Fig. 61).

Distribution. Berlese (1903) records the type habitat as follows : " in foliis putrescentibus in hortis ad ' Firenze ', perfrequens ". I have examined

specimens from deciduous litter, St. Peter's Valley, Jersey ; from oak leaf-mould, Forest of Dean, Gloucester and from humus, Cornwall.



Figs. 57–61.—*Iphidozercon gibbus* (Berlese), female. 57. Dorsum ; 58. Lateral view ; 59. Vertex ; 60. Venter ; 61. Chelicera.

IPHIDOZERCON MINUTUS (Halbert)

Sciulus minutus Halbert, J. N. (1915). Proc. Roy. Irish Acad. **39** (ii) : 76, fig.
Lasioscius (*Lecioscius*) *minutus* Halbert, J. N. (1923). J. Linn. Soc. Lond. Zool. **25** : 374.
Arctosciopsis minutus Evans, G. O. (1954). Proc. zool. Soc. Lond. **123** : 797, figs.

The redescription of this species by Evans (1954) is adequate for its identity. The dorsal shield bears thirty-two pairs of setae and not thirty-five pairs as stated in that work—some of the setae figured on the lateral margins of the dorsal shield actually belong to the marginal series which are situated on the integument.

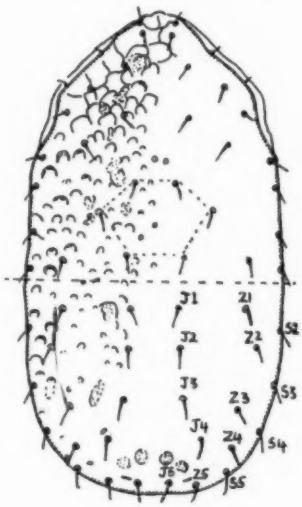
Distribution. This species has been recorded from sphagnum, Clare Island (Halbert, 1915) and from a salt marsh in South Wales (Evans, 1954).

IPHIDOZERCON CORTICALIS, sp. n.

Females. Dorsal shield (330 × 170 μ) with thirty-two pairs of simple setae of which fourteen pairs are situated on the " posterior dorsal shield "

(Fig. 62). Vertex directed downwards, vertical setae simple, not visible when mite is seen from above (Fig. 63). Dorsal shield without median elevation, surface of shield with large punctures in its anterior two-thirds.

Sternal shield narrow with three pairs of setae. Metasternals free ; genital shield very narrow without setae. Anal shield with rounded anterior margin and well-separated from genital shield (Fig. 64). Chaetotaxy of the region posterior to coxae IV as figured. Peritrematal shield as in *gibbus* ; peritreme with a U-shaped bend near the vertex.



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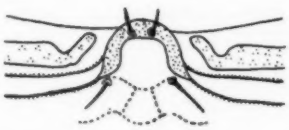

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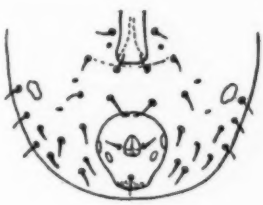

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Figs. 62–64.—*Iphidozercon corticalis* sp. n., female. 62. Dorsum ; 63. Vertex ; 64. Anal region.

Gnathosoma normal ; tectum trispinate. Fixed digit of the chelicera with two or three weak teeth ; movable digit bidentate.

Legs short but all with pretarsi and ambulacra.

Locality. A single female (Holotype : 1957 : 11 : 22 : 9) from bark of fruit tree, Gt. Braxted, near Witham, Essex (coll. D. A. Chant).

Genus *LASIOSEIUS* Berlese

Lasioseius Berlese, A. (1916). Redia **12** : 34.
Aceosejus Sellnick, M. (1941). Zool. Anz. **133** : 149 *syn. nov.*
Boringuolaelaps Fox, I. (1946). J. Parasit. **32** : 450.

Type : *Seius muricatus* Berlese, 1887 nec C. L. Koch, 1839.
(=*Typhlodromus berlesei* Oudemans, 1938).

The species included in this genus are closely related to members of the genus *Melichares* in the chaetotaxy of the dorsum and the form of the ventral shields. The fundamental difference between them lies in the structure of the gnathosoma which in *Lasioseius* has the corniculi relatively short and widely

separated distally, and the ventral groove provided with five or more transverse rows of denticles (Fig. 5). The marginal series of setae on the dorsum is always present but in the region of the " anterior dorsal shield " may be partially or completely fused with the shield. In the former condition, only two pairs of setae occur on the membrane lateral to the shield. The " posterior dorsal shield ", on the other hand, never has more than fifteen pairs of setae although in some species this number may be decreased through the loss of one or more pairs in the dorsal series (J.). The dorsal setae may be simple, pilose or lanceolate.

The venter of the female is well-sclerotised with the sternal shield, except in *L. muricatus* which has jugularia, bearing three pairs of setae. The posterior margin of the shield may be truncate or concave. Each metasternal seta usually lies on a platelet. The wedge-shaped genital shield with a pair of setae lies in close proximity to the ventri-anal shield which carries from two to six pairs of preanals. The venter of the male is covered by a sterniti-genital shield with four or five pairs of setae depending on the presence or absence of jugularia and a separate ventri-anal shield.

The tectum has a tri- or multidentate anterior margin. The fixed digit of the chelicera, in the majority of the known species is provided with a row of closely-set teeth along the greater part of its length. The spermatophoral process is usually simple.

All legs terminate in ambulacra ; leg II of the male is unarmed.

The characters upon which Sellnick based his genus *Aceosejus*, namely the presence of jugularia in the female and a sclerotised tubercle on the ventri-anal shield of the male, are not considered of sufficient importance to warrant the separation of this genus from *Lasioseius*. The type species of *Aceosejus*, *L. muricatus*, is a typical member of the genus *Lasioseius* in the structure and chaetotaxy of the dorsum, the form of the gnathosoma and chelicerae, and in the sclerotisation of the venter.

Key to females of the British species of Lasioseius *Berlese*

1.	With large, strongly sclerotised jugularia ; " anterior dorsal shield " with twenty-three pairs of setae, " posterior dorsal shield " with fifteen pairs (Fig. 68) ; setae near the posterior margin of the dorsal shield long, spinose. On *Polyporus*..	*L. muricatus* (C. L. Koch)
–.	Without jugularia although pre-endopodal shields may be present ; " anterior dorsal shield " with not more than twenty-one pairs of setae	2.
2.	" Posterior dorsal shield " with only three pairs of setae in the dorsal series (J)—Fig. 65	*L. berlesei* Oudemans.
–.	" Posterior dorsal shield " with five pairs of setae in the dorsal series (Fig. 69)	3.
3.	Posterior margin of the sternal shield in the female deeply incised to about the level of sternal setae II (Fig. 71).....	4.
	Posterior margin of the sternal shield truncate or slightly concave (Fig. 73).....	5.
4.	First pair of sternal setae short, spine-like (Fig. 71) ; dorsal setae smooth ; ventri-anal shield with two pairs of preanal setae	*L. bispinosus* sp. n.

–. First pair of sternal setae simple ; dorsal setae serrate-lanceolate, especially towards the posterior end of the dorsal shield ; ventri-anal shield with four pairs of preanal setae .. *L. ometes* (Oudemans).

5. Dorsal setae smooth, those near the posterior margin of the dorsal shield strong and spinose (Fig. 72) ; " anterior dorsal shield " with nineteen pairs of setae ..... *L. confusus* sp. n.

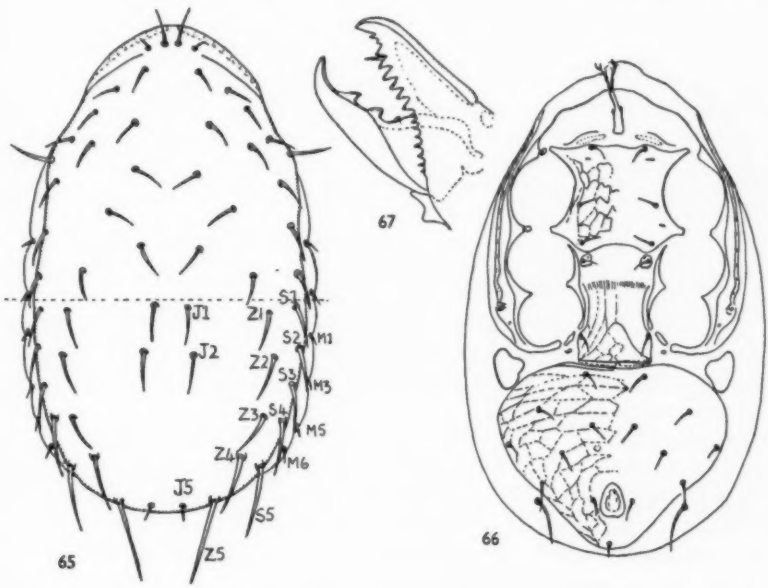
6. Dorsal setae serrated, those near the posterior margin lanceolate (Fig. 69) ; " anterior dorsal shield " with twenty-one pairs of setae ..... *L. penicilliger* Berlese.

LASIOSEIUS BERLESEI (Oudemans)

Seius muricatus Berlese, A. (1887). Acari. Myriopoda et Scorpiones etc. Padua. Fasc. 41 No. 6.
Typhlodromus berlesei Oudemans, A. C. (1938). Tijdschr. Ent. **81** : II (nom. nov. pro *Seius muricatus* Berlese nec Koch, 1839).
Lasioseius berlesei Oudemans, A. C. (1939). Zool. Anz. **126** : 303.
Lasioseius aba Baker, E. W. & Wharton, G. W. (1952). Introduction to Acarology. New York : 88.

The original description and figures of this species given by Berlese (1887) are inadequate for its specific identity. The following redescription of the female is based on specimens compared with the type material in the Berlese Collection at Florence.

Female. The dorsal shield (approx. $460 \times 275\,\mu$) is reticulated and carries thirty-one pairs of setae of which eighteen pairs are situated on the " anterior dorsal shield " (Fig. 65). The most characteristic feature of the chaetotaxy of the shield is the presence of only three pairs of setae in the J



Figs. 65–67.—*Lasioseius berlesei* (Oudemans), female. 65. Dorsum ; 66. Venter ; 67. Chelicera.

series of the " posterior dorsal shield ". The distribution of the marginal setae on the lateral interscutal membrane is shown in the figure.

The sternal shield bears the usual three pairs of setae with the metasternals free. There is some indication of sclerotisation anterior to the sternal shield. The wedge-shaped genital shield lies in close proximity to the anterior margin of the ventri-anal shield (approx. 165 × 220 μ), which has six pairs of preanals in addition to the three setae normally associated with the anus. The metapodal shields are large and conspicuous (Fig. 66). The peritrematal shield is fused with the exopodal shields in the region of coxa IV. The endopodals are well developed in the region of coxa III and IV. The laciniae of the tritosternum are pilose.

The venter of the gnathosoma is shown in Fig. 5. The tectum has its anterior margin multidentate. The fixed digit of the chelicera has a row of small, closely-set teeth along its entire length ; the movable digit is tridentate with the posterior tooth relatively small (Fig. 67).

All legs terminate in ambulacra ; there are no macrosetae on tarsus IV.

Distribution. This species has been recorded from a number of localities on the Continent (Berlese, 1887 ; Franz, 1954 and Willmann, 1954). I have examined specimens collected in leaf-mould near a pond at Woking, Surrey (coll. M. E. Bacchus) and under bark of a fallen elm tree at Harefield, Middlesex (coll. A. H. G. Alston).

LASIOSEIUS MURICATUS (C. L. Koch)

Sejus muricatus Koch, C. L. (1839). Deutsch. Crust. Myr. Arach. fasc. 24, t. 11.
Laelaps (?) *ligoniformis* Michael, A. D. (1892). Trans. Linn. Soc. Zool. **5** : 316 figs. *syn. nov.*
Ameroseius pseudocometa Schweizer, J. (1922). Verh. Naturf. Ges. Basel **33** : 42 fig.
Aceosejus muricatus, Sellnick, M. (1941). Zool. Anz. **133** : 149 figs.

Female. A large strongly sclerotised species. Dorsal shield (approx. 560 × 380 μ) reticulated and punctured with thirty-eight pairs of setae (Fig. 68). " Anterior dorsal shield " with twenty-three pairs of setae. Setae of rows Z and S on the " posterior dorsal shield " spinose and situated on tubercles. Paravertical setae very short.

Jugularia, large, strongly sclerotised. Sternal shield punctured and with two pairs of simple setae. Metasternals free. Wedge-shaped genital shield with a pair of setae. Four platelets between genital and large ventri-anal (260 × 340 μ). The latter with six pairs of preanals. Peritrematal shield large, fused with the exopodal shield in the region of coxae IV. Peritremes extending as far as the paravertical setae. Endopodal shields well developed in the region of coxae III and IV.

Gnathosoma normal for the genus. Corniculi widely separated distally ; rostral setae simple. Tectum produced into three processes, external margin of the lateral processes and the anterior margin of the median process minutely denticulate. Fixed digit of the chelicera with four or five strong teeth.

All legs with pretarsi and ambulacra. Macroseta on tarsus IV.

Male. Chaetotaxy and ornamentation of the dorsal shield and lateral interscutal membrane essentially the same as in the female.

Sterniti-genital shield with five pairs of setae (no jugularia). Ventri-anal shield with seventeen setae and a strongly sclerotised bifid elevation near its anterior margin. (I can see no evidence of this projection bearing genital suckers as Baker & Wharton (1951) have stated.)

The gnathosoma is the same as in the female except that the corniculi are slightly convergent. The fixed digit of the chelicera is slender and has a row of closely-set teeth along its cutting edge. The unidentate movable digit has a large spermatophoral process.

All legs with pretarsi and ambulacra. Femur IV with a stout spine on its posterior margin.

Distribution. On *Polyporus* in Germany, Switzerland and the British Isles.

LASIOSEIUS OMETES (Oudemans)

Hypoaspis ometes Oudemans, A. C. (1903). Ent. Ber. **1** : 100 ; Oudemans, A. C. (1904). Tijdschr. Ned. Dierk. Ver. Ser. 2, **8** : 203, figs.

Lasioseius ometes, Halbert, J. N. (1923). J. Linn. Soc. Lond. Zool. **25** : 3.

Lasioseius (Zercoseius) ometes, Vitzthum, H. G. (1923). Arch. Naturgesch. **89A** Heft 2 : 110, figs.

Female. Dorsal shield (approx. 585 × 300 μ) strongly sclerotised, reticulated and bearing thirty-six pairs of serrated or lanceolate-pencillate setae. " Posterior dorsal shield " with the usual fifteen pairs of setae distributed in six longitudinal rows of five setae.

Pre-endopodal shields well developed ; sternal shield with three pairs of setae, posterior margin deeply incised to the level of sternal setae II. Metasternal setae on the integument, genital shield punctured and with the usual pair of setae. Integument between the genital and ventri-anal shield with four distinct platelets. Ventri-anal shield (176 × 240 μ) punctured in its posterior half and with four pairs of preanal setae. Two pairs of metapodalia conspicuous. Peritrematal shield fused with the exopodal shield posteriorly. Peritreme reaching to the anterior margin of coxa I.

Gnathosoma normal for the genus. Tectum with a denticulate anterior margin. Fixed digit of the chelicera with a row of closely-set teeth.

All legs with pretarsi and ambulacra.

Distribution. This species has been previously recorded from the Netherlands, Germany and Ireland. It has been found in sweepings from a floor in a house, in tunnels of wood-boring beetles and under bark of decaying logs. The Collections of the British Museum (Natural History) contain a single female from mixed deciduous litter, S.E. England.

LASIOSEIUS PENICILLIGER Berlese

Lasioseius (Zercoseius) penicilliger Berlese, A. (1916). Redia **12** : 44.

Female. Dorsal shield (approx. 570 × 310 μ) strongly sclerotised, reticulate-scabrid and bearing thirty-six pairs of serrated setae of which those in the posterior third of the shield tend to be lanceolate (Fig. 69). Z5 about 65 μ in length. With two pairs of marginal setae on the membrane lateral to the " anterior dorsal shield ".

Pre-endopodal shields weakly sclerotised. Sternal shield with its posterior margin slightly concave and bearing three pairs of setae. Metasternal setae on platelets ; genital shield normal. Integument between the genital and ventri-anal shields with four platelets which in some specimens appear to fuse and form a single sclerotised strip. The ventri-anal shield (220 × 265 μ) has six pairs of preanal setae. The two pairs of metapodalia are conspicuous. Peritrematal shield fused with the exopodal shield posteriorly.

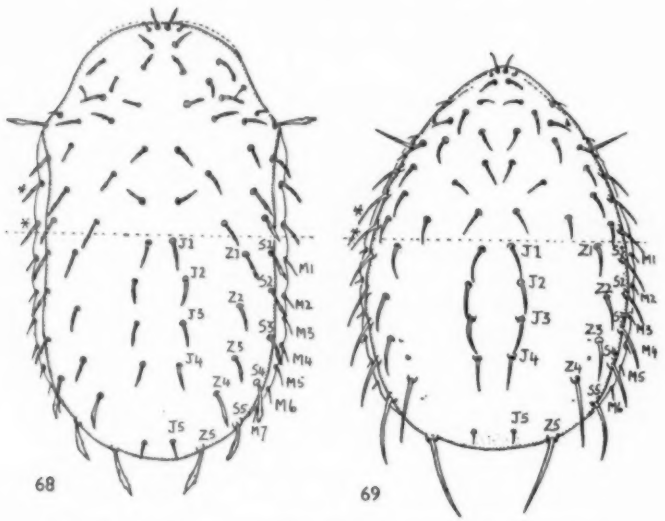


Fig. 68.—*Lasioseius muricatus* (C. L. Koch), female. Dorsum.
Fig. 69.—*Lasioseius penicilliger* (Berlese), female. Dorsum.

Gnathosoma normal for the genus. Tectum with a truncate anterior margin denticulate. Fixed digit of the chelicera with a row of teeth along its cutting edge.

All legs with pretarsi and ambulacra. Tarsus IV without macroseta.

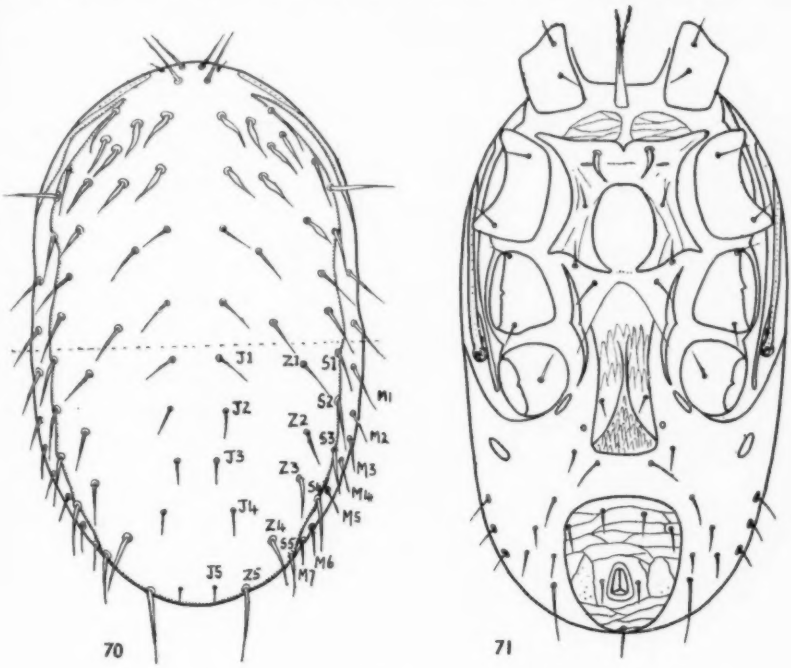
Distribution. Berlese (1916) gives the habitat of this species as " in agro patavino, sub lignis putribus, ad terram ". Sheals (1956) has found this species in old grassland at Glasgow.

LASIOSEIUS BISPINOSUS, sp. n.

Female. Dorsal shield (460 × 275 μ) relatively weakly sclerotised and finely reticulate bearing thirty-six pairs of smooth setae ; those on the anterior third of the shield enlarged in their basal halves (Fig. 70). " Posterior dorsal shield " with fifteen pairs of setae arranged as in the figure. The marginal series lie off the dorsal shield in the region of its posterior two-thirds.

Sternal shield and pre-endopodal shields unusual in form (Fig. 71). Posterior margin of sternal shield deeply incised and bearing only two pairs of setae of which the anterior pair are stout and spine-like. The ventri-anal shield about

as long (100 μ) as broad and with only two pairs of preanal setae. Only one pair of large metapodal shields. Integument posterior to coxae IV with twenty setae. Peritrematal shield fused with the exopodal shield posteriorly.



Figs. 70–71.—*Lasioseius bispinosus* sp. n., female. 70. Dorsum ; 71. Venter.

Gnathosoma normal for the genus. Tectum with a denticulate anterior margin. Fixed digit of the chelicera with a row of about eleven teeth along its cutting edge.

All legs with pretarsi and ambulacra.

Distribution. A single female collected on mahogany logs (imported) in Glasgow (Holotype : 1957 : 11 : 22 : 1). This species was sent to me for identification by Dr A. M. Hughes.

LASIOSEIUS CONFUSUS, sp. n.

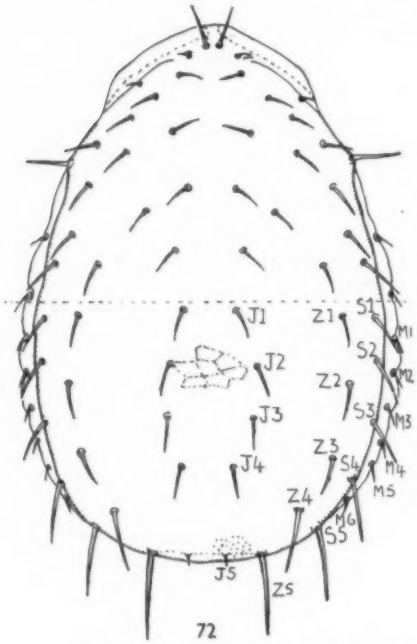
Female. A strongly sclerotised species. Dorsal shield (approx. 520 × 325 μ) reticulated and punctured in its posterior half (Fig. 72). It carries thirty-four pairs of setae distributed as in the figure. " Posterior dorsal shield " with fifteen pairs of setae, those towards the posterior end of the shield strong, spine-like and inconspicuously spiculate.

Pre-endopodal shields weakly sclerotised ; sternal shield punctured and bearing three pairs of setae. Metasternal setae on platelets. Genital shield with a pair of setae and posterior to it four platelets (Fig. 73). Ventri-anal

shield large (189 × 270 μ) and bearing six pairs of preanal setae. Metapodalia large. Peritrematal shield fused with the exopodal shield posteriorly.

Gnathosoma normal for the genus. Tectum produced into three processes. Fixed digit of the chelicera with a row of closely-set teeth along its cutting edge.

All legs with pretarsi and ambulacra.



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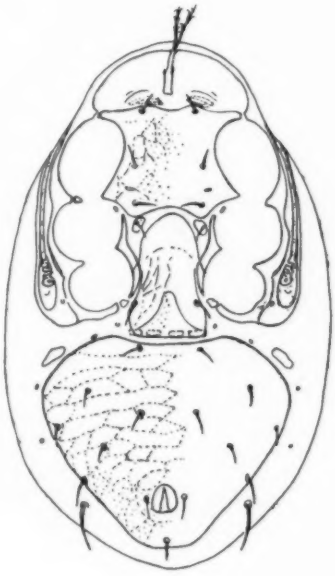

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Figs. 72–73.—*Lasioseius confusus* sp. n., female. 72. Dorsum ; 73. Venter.

Distribution. Four females (Holotype : 1957 : 11 : 22 : 28 ; Paratypes : 1957 : 11 : 22 : 45–47) from roots of rushes by Big Pool, St. Agnes, Isles of Scilly, Cornwall (coll. K. H. Hyatt, 1957). Five females (Paratypes : 1957 : 11 : 22 : 29–33) in Spagnum " Borth Bog " (Cors Fochno) N. Cardiganshire, Wales (coll. G. O. Evans). This species superficially resembles (and has probably been confused with) *L. berlesei*. It differs from that species in having five pairs of setae in the J. series, punctures on the posterior half of the dorsal shield and a trispinate tectum.

SYNONYMIC LIST OF THE SPECIES OF THE SUBFAMILY ACEOSEJINAE

The following synonymic list of the known species of the subfamily is probably incomplete since a number of species inadequately described by older authors may be found, on the examination of the type material, to belong here. It will be noted that two genera (?) not occurring in the British fauna, *Hoploseius* Berlese and *Zygoseius* Berlese, are included.

Genus *ARCTOSEIUS* Berlese

Arctoseius bicuspidatus Willmann, 1949. Abh. naturw. Ver. Bremen **32** : 355, fig.
Distribution : Bavaria.
Lasioseius cetratus Sellnick, 1940. Göteborgs Vetensk-Samh. Handl. (5), **6B** : 29, 99, figs. ♀. syn. : *Arctoseius bispinatus* Weis-Fogh.
Distribution : Iceland, Europe.
Gamasellus (*Sessiluncus*) *eremita* Berlese, 1918. Redia **13** : 137.
syn. : *Arctoseius austriacus* Willmann, 1949. *syn. nov.*
Distribution : Italy, Austria.
Arctoseius halophilus Willmann, 1949. Abh. naturw. Ver. Bremen **32** : 354, figs.
Distribution : Poland.
Arctoseius laterincisus* Sig Thor, 1930. Skr. Svalbard Ishavet Oslo **27 : 112, pls.
Distribution : Spitzbergen.
Arctoseius limburgensis Nesbitt, 1954. Natuurh. Maanbl. **43** : 20, figs. ♀.
Distribution : Netherlands.
Arctoseius magnanalis Evans, *sp. nov.*
Distribution : England.
Arctoseius multidentatus Evans, 1955. Bull. Brit. Mus. (nat. Hist.) Zool. **2** : 291, figs. ♀.
Distribution : Alaska.
Arctoseius oculatus Willmann, 1949. Abh. naturw. Ver. Bremen **32** : 350.
Distribution : Austria.
Arctoseius ornatus Evans, 1955. Bull. Brit. Mus. (nat. Hist.) Zool. **2** : 289, figs.
Arctoseius pratensis Hirschmann, 1954. In Franz, Spiegel Land-Teirwelt **1** : 350. NOM. NUD.
Laelaps (*Iphis*) *semiscissus* Berlese, 1892, A.M.S., Fasc. 63, No. 7.
Distribution : Italy.
Arctoseius weberi Evans, 1955. Bull. Brit. Mus. (nat. Hist.) Zool. **2** : 291, figs.

Genus *HOPLOSEIUS* Berlese

It is possible that the genus *Lasioseius* Berlese is synonymous with *Hoploseius*.
Zercon cometa* Berlese, 1910. Redia **6 : 373.
Distribution : Java.

Genus *IPHIDOZERCON* Berlese

Iphidozercon corticalis Evans, *sp. nov.*
Distribution : England.
Eviphis gibbus* Berlese, 1904. Redia **1 : 246.
Distribution : Italy, British Isles.
Lasioseius insularis Willmann, 1952. Veroff. Inst. Meeresforsch. Bremerhaven **1** : 147, figs. ♀.
Distribution : Germany.

Seiulus minutus Halbert, 1915. Proc. R. Irish Acad. **31**, 39 ii : 76, fig.
Distribution : British Isles.
Lasioseius (*Lasioseius*) *pulvisculus* Berlese, 1921. Redia **14** : 171, ♀.
Distribution : Italy.
Lasioseius (*Leioseius*) *venustulus* Berlese, 1917. Redia **12** : 45, ♂♀.
Distribution : Italy.

Genus *LASIOSEIUS* Berlese

Typhlodromus berlesei* Oudemans, 1938. Tijdschr. Ent. **81 : 2.
syn. : *Lasioseius aba* Baker and Wharton, 1952.
Distribution : Europe.
Lasioseius (*Zercoseius*) *boomsmai* Womersley, 1956. J. Linn. Soc. Lond. Zool. **42** : 545, figs.
Distribution : Australia.
Lasioseius confusus Evans, *sp. nov.*
Distribution : British Isles.
Lasioseius bispinosus Evans, *sp. nov.*
Distribution : British Isles (?imported).
Hypoaspis ometes Oudemans, 1903. Ent. Ber. Amst. No. 14 : 100.
Distribution : Europe.
Laelaps mexicanus Banks, 1905. Proc. ent. Soc. Washington **7** : 138.
Distribution : Mexico.
Sejus muricatus C. L. Koch, 1839. Deutsch. Crust. Myr. Arach. fasc. 24, t. 11.
syn. : *Laelaps* (?) *ligoniformis* Michael, 1892, *syn. nov.*; *Ameroseius pseudocometa* Schweizer, 1922, *syn. nov.*
Distribution : Europe.
Lasioseius muricatus var. *floridensis* Berlese, 1918. Redia **13** : 190. NOM. NUD.
Lasioseius muricatus var. *transoceanicus* Berlese, 1918. Redia **13** : 190. NOM. NUD.
Lasioseius (*Zercoseius*) *podocinoides* Berlese, 1917. Redia **12** : 43.
Distribution : East Africa.
Lasioseius (*Zercoseius*) *penicilliger* Berlese, 1916. Redia **12** : 44.
Distribution : Italy and British Isles.
Lasioseius (*Zercoseius*) *penicilliger* var. *floridensis* Berlese, 1917. Redia **12** : 44.
syn. : *Borinquolaelaps dentatus* Fox, 1946.
Distribution : U.S.A. and Puerto Rico.
Platyseius queenslandicus Womersley, 1956. J. Linn. Soc. Lond. Zool. **42** : 550, fig. ♀.
Distribution : Australia.
Lasioseius (*Zercoseius*) *paliger* Berlese, 1916. Redia **12** : 43.
Distribution : Italy.
Lasioseius (*Zercoseius*) *sublaevis* Berlese, 1916 (1917). Redia **12** : 44.
Distribution : Java.
Lasioseius (*Zercoseius*) *thermophilus* Willmann, 1942. Zool. Anz. **139** : 242.
Distribution : Germany.

Genus *LEIOSEIUS* Berlese

Leioseius elongatus Evans, sp. nov.
Distribution : England.
Arctoseius (*Arctoseiodes*) *ibericus* Willmann, 1949. Abh. naturw. Ver. Bremen **32** : 356, figs.
Distribution : Spain and British Isles.
Ameroseius minusculus* Berlese, 1905. Redia **2 : 235.
Distribution : Italy and U.S.A. (Connecticut).
Lasioseius salinus Halbert, 1920. Proc. R. Irish Acad. **35** : 125, fig.
Distribution : British Isles and Germany.

Genus *MELICHARES* Hering, *s. lat.*

Subgenus *Melichares* Hering, *s. str.*
Melichares agilis* Hering, 1838. Acta. Acad. Caes. Leop. Car. Nat. Cur. **18 : 620, figs.
syn. : *Typhlodromus domesticus* Oudemans, 1929.
Distribution : Europe.
Subgenus *Blattisocius* Keegan.
Lasioseius (Lasioseius) *tarsalis* Berlese, 1918. Redia **13** : 134.
syn.: *Typhlodromus tineivorus* Oudemans, 1929, *syn. nov.*; *Blattisocius triodons* Keegan, 1944 ; *Lasioseius similis* Schweizer, 1949, *syn. nov.*
Distribution : Cosmopolitan.
Blattisocius keegani Fox, 1947. Ann. ent. Soc. Amer. **40** : 599, fig. ♀.
Distribution : North and Central America, Europe and South-east Asia.
Typhlodromus mali Oudemans, 1929. Ent. Ber. Amst. **8** : 30.
Distribution : Europe.
Lasioseius dentriticus Berlese, 1918. Redia **13** : 133, ♂ ♀.
syn.: *Lasioseius fimbriatus* Halbert, 1923, *syn. nov.*; *Seiulus amboinensis* Oudemans, 1925, *syn. nov.*
Distribution : Cosmopolitan.
Garmania (*Paragarmania*) *urticana* Nesbitt, 1954. Natuurh. Maandbl. **43** : 22, figs. ♀.
Distribution : Netherlands.

Genus *PROCTOLAELAPS* Berlese

Proctolaelaps s. str.

Lasioseius (*Lasioseius*) *aurora* Vitzthum, 1925. Suppl. Ent. Berlin no. **11** : 24, figs.
Distribution : Sumatra.
Amblyseius (*Seiopsis*) *brevipilus* Berlese, 1924. Redia **15** : 256.
Distribution : Japan.
Lasioseius brevisternus Berlese, 1916. Redia **12** : 38.
Distribution : Italian Somaliland.
Lasioseius consocius Berlese, 1916. Redia **12** : 39.
Distribution : La Plata.

Lasioseius conviva Berlese, 1916. Redia **12** : 38.
Distribution : Java.
Lasioseius conviva var. *laevisternus* Berlese, 1916. Redia **12** : 39.
Distribution : Java.
Gamasus cossi Dugès, 1834. Ann. Sci. nat. Paris Zool. (2) **1** : 19.
Distribution : Netherlands.
Lasioseius (*Lasioseius*) *eccoptogasteris* Vitzthum, 1923. Arch. Naturgesch. **89A** (2) : 108, figs.
Distribution : Austria.
Lasioseius fissuratus Berlese, 1916. Redia **12** : 37.
Distribution : La Plata.
Lasioseius fissuratus var. *nostras* Berlese, 1916. Redia **12** : 38.
Distribution : Italy.
Hypoaspis hypudaei Oudemans, 1902. Tijdschr. Ent. **45** : 21, figs.
syn. : *Lasioseius innumerabilis* Berlese, 1918, *syn. nov.*; *Typhlodromus bulbicolus* Oudemans, 1929 ; *Lasioseius alpinus* Schweizer, 1949, *syn. nov.*; *Lasioseius ventritrichosus* Schweizer, 1949, *syn. nov.*
Distribution : Cosmopolitan.
Lasioseius (*Lasioseius*) *hystrix* Vitzthum, 1923. Arch. Naturgesch **89A** (2) : 105, figs.
Distribution : Austria.
Garmania lewisi Garman & McGregor, 1956. Bull. S. Calif. Acad. Sci. **55**, 7, figs. ♂.
Syn : *Garmania garmanis* McGregor, 1956 (teste D. A. Chant).
Distribution : U.S.A.
Blattilaelaps nauphoetae Womersley, 1956. J. Linn. Soc. Lond. Zool. **42** : 566, figs. ♂ ♀.
Distribution : Queensland.
Garmania nesbitti Womersley, 1956. J. Linn. Soc. Lond. **42** : 548, figs. ♀.
Distribution : Queensland.
Seiulus novaeguineae Oudemans, 1905. Ent. Ber. Amst. **1**, No. 23 : 222.
Distribution : New Guinea.
Typhlodromus pomorum Oudemans, 1930. Ent. Ber. Amst. **8** : 31.
Distribution : Holland.
Proctolaelaps productus* Berlese, 1924. Redia **15 : 255.
Distribution : East Africa.
Proctolaelaps (*Proctolaelaps*) *robustus* Evans, *sp. nov.*
Distribution : Scotland.
Proctolaelaps (*Proctolaelaps*) *scolyti* Evans, *sp. nov.*
Distribution : England.
Garmania vandenbergi Ryke, 1954. J. ent. Soc. S. Afr. **17** : 241, figs. ♀♂.
syn. : *Garmania protaea* Ryke, 1954, *syn. nov.*
Distribution : South Africa.

Subgenus *Neojordensia* Evans.

Proctolaelaps (*Neojordensia*) *lawrencei* Evans, *sp. nov.*
Distribution : England.

***Seiulus levis* Oudemans and Voigts, 1904. In Voigts and Oudemans, Zool. Anz. 27 : 654.**
Distribution : Europe.

Genus *ZERCOSEIUS* Berlese

***Seius spathuliger* Leonardi, 1899. In Canestrini. Prosp. Acarof. Ital. 8 : 923, fig. ♀.**
syn. : *Ameroseius zerconiformis* Berlese, 1905.
Distribution : Europe.

Genus *ZYGOSEIUS* Berlese

***Lasioseius* (*Zygoseius*) *alter* Vitzthum, 125. Suppl. Ent. Berlin. No. 11 : 23, figs.**
Distribution : Sumatra.
****Lasioseius* (*Zygoseius*) *furciger* Berlese, 1916. Redia 12 : 41.**
Distribution : South America and South Africa.

SUMMARY

1. This paper deals with a revision of the British species of the subfamily Aceosejinae together with a synonymic list of the species of the subfamily.

2. Keys are given for the separation of genera and species of the British aceosejines.

3. The following new synonymy is introduced :

(a) *Arctoseiulus* Willmann and *Arctotarseius* Willmann are synonyms of *Arctoseius* Sig Thor.
(b) *Arctoseiodes* Willmann is a synonym of *Leioseius* Berlese.
(c) *Seiopsis* Berlese, *Jordensia* Oudemans and *Blattilaelaps* Womersley are synonyms of *Proctolaelaps* Berlese.
(d) *Garmania* Nesbitt and *Paragarmania* Nesbitt are synonyms of *Melichares* Hering.
(e) *Arctoseiopsis* Evans is a synonym of *Iphidozercon* Berlese.
(f) *Aceosejus* Sellnick is a synonym of *Lasioseius* Berlese.
(g) *Lasioseius* (*L.*) *innumerabilis* Berlese, *Lasioseius alpinus* Schweizer and *Lasioseius ventritrichosus* Schweizer are synonyms of *Hypoaspis hypudaei* Oudemans.
(h) *Typhlodromus domesticus* Oudemans is a synonym of *Melichares agilis* Hering.
(i) *Typhlodromus tineivorus* Oudemans, *Blattisocius triodons* Keegan and *Lasioseius similis* Schweizer are synonyms of *Lasioseius* (*L.*) *tarsalis* Berlese.
(*j*) *Lasioseius fimbriatus* Halbert and *Seiulus amboinensis* Oudemans are synonyms of *Lasioseius* (*L.*) *dentriticus* Berlese.
(k) *Laelaps ligoniformis* Michael is a synonym of *Sejus muricatus* C. L. Koch.
(l) *Arctoseius austriacus* Willmann is a synonym of *Gamasellus* (*Sessiluncus*) *eremita* Berlese.

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A STUDY OF SOME DEVELOPMENTAL STAGES OF THE THELYCUM AND ITS RELATION TO THE SPERMATOPHORES IN THE PRAWN *PENAEUS JAPONICUS* BATE *

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(With 11 figures in the text)

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INTRODUCTION

Very little has been published on the genitalia of penaeid prawns, except for taxonomic descriptions which are often imperfect. The purpose of the present paper is to elucidate the development of the thelycum in the female of *Penaeus japonicus* Bate and its relation to the spermatophores.

MATERIAL

The material used was, for the most part, collected recently in the Arabian Sea, off Karachi and off Dacca in the Bay of Bengal. Fortunately the thelycum was in a different stage of development in each of the females collected. The largest female had no external signs of impregnation but, when the ventral wall of the thelycum was removed in order to study the nature of the dorsal wall, the incomplete spermatophores were then seen (Fig. 2, *st.*). Since little is known about the relation of the spermatophores to the thelycum, much of the walls of the spermsacs were removed in the supposition that it was the membranous wall of the seminal receptacle (Hudinaga, 1942). This, at any rate, helped to study the internal skeleton of the spermsacs and its relation to the anterior plate of the thelycum. The complete spermatophores (Figs. 8 and 9) were removed by dissection from a female in the Paris Museum and I was allowed to keep them by kind permission of the authorities.

* Part of a thesis accepted for the degree of D. Phil. (Oxon).

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HISTORY

The first mention of the thelycum in *Penaeus japonicus* Bate, under the name of *Penaeus canaliculatus* Olivier, was made by de Haan (1849). He described it as " . . . between the fourth [pair of legs] a narrow horny rounded lobe ; between the fifth, a broader circular lobe, split in front of the middle and embracing the median spine " (translated). Bate (1888) however, was the first to recognise the specific importance of this structure and named it the *thelycum* (p. 244). Since that time this organ has attracted the attention of many zoologists.

Before proceeding further it seems necessary to know the exact implication of the term thelycum. When proposing it (p. 245) Bate said that it is " . . . the peculiar formation of the complementary external female apparatus ". Generally speaking the thelycum consists of a series of prominences, depressions or grooves, plates and sacs raised from the sternites of the sixth to eighth thoracic segments. In *P. japonicus*, however, it consists of a triangular projection, the anterior plate, on the seventh thoracic sternite and a sac or pouch-like structure on the eighth. But when he applied this term in describing the two " Challenger " females he said that " . . . between the posterior pair of pereiopoda, is a large thelycum " (p. 247). Here the anterior plate is not mentioned at all. The reason presumably is the presence in his specimen of enormous wings of the spermatophores. These, when present, completely mask the plate in question and Bate erroneously took them to be a part of the thelycum. But from his definition given above and, since the plate is functionally a part of the " complementary external female apparatus (as shown by Heldt, 1939, p. 61 in the case of *Penaeus trisulcatus* Leach, and as will be seen later in this paper), it should therefore be included in the term thelycum, as Kubo (1949) for example has done. And so the term thelycum must be held to apply in *P. japonicus* to both the plate and the pouch.

It may be pointed out here that many authors refer to the pouch of *P. japonicus* as the seminal receptacle. This term is somewhat misleading since the cavity of the pouch is used only for holding the stoppers or the wings of the spermatophores while the actual sperm sacs are inserted between the anterior plate and the body wall (Figs. 2 and 10). Kishinouye (1900) gave a better description and figures of the thelycum and correctly identified the wing-like structures in the thelycum as the spermatophores.

In 1942, Hudinaga in his paper on the reproduction, development and rearing of *P. japonicus* gave an account of the internal structure of the thelycum and the position of the spermatophores in it. A comparative study on the thelycum of penaeids was made by Kubo (1949) and he, for the first time, reported some developmental stages of the thelycum of many species including *P. japonicus*.

DESCRIPTION OF THE THELYCUM

At first sight (as seen from the ventral surface) the adult thelycum is as represented in Fig. 1. Anteriorly, between the bases of peraeopods IV, is a narrowly triangular plate (*a*) with lateral margins setose and the surface markedly concave. Behind this is a large pouch-like structure (*b*) covering

the entire space between the bases of peraeopods IV and V. The walls of the pouch are comparatively soft and there is a long slit-like entrance anteriorly (*o*). Posterior to the pouch is a strongly chitinized ridge (*c*).

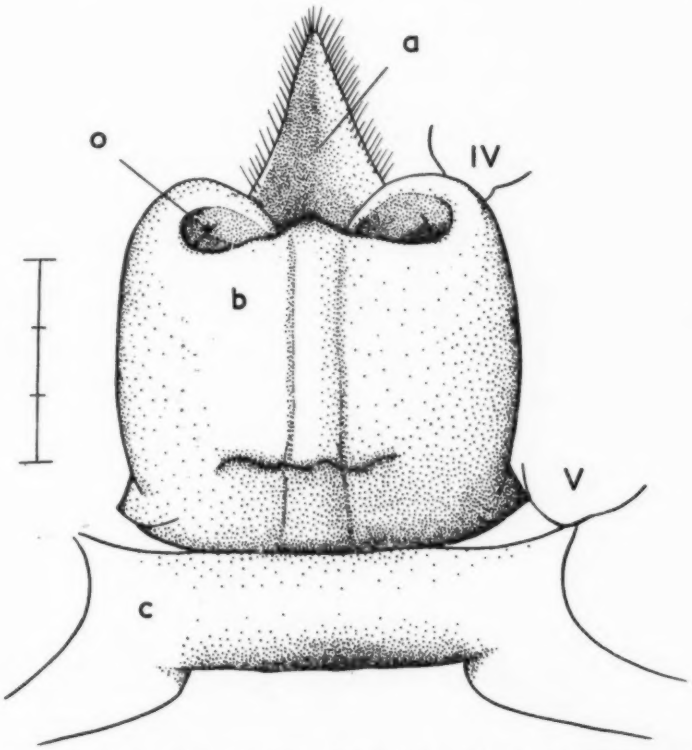
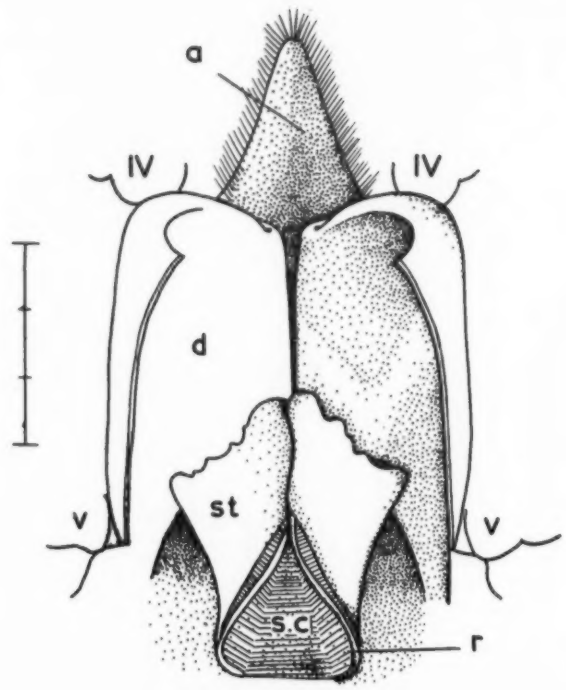


Fig. 1.—*Penaeus japonicus* Bate. Thelycum of an adult female (carapace length = 47 mm.) from the Arabian Sea, in ventral aspect. *a*. Anterior portion of the shield on the triangular protuberance of the seventh thoracic sternite. *b*. Ventral wall of the pouch. *c*. Transverse ridge posterior to the pouch. *o*. Slit like entrance to the pouch. IV and V. Bases of peraeopods IV and V respectively. (Scale = 3 mm.).

In Fig. 2 the ventral wall of the pouch and the ridge posterior to it have been removed (the cut lateral edges are represented by double lines) to show the two separate halves of the dorsal wall and the bases of the incomplete stoppers of the spermatophores (*st*). The two halves of the dorsal wall, the infoldings, are clearly indicated in the figure (*d*) ; the inner margins are closely apposed throughout the distal two-thirds of their length, and diverge proximally to form an arch (see Fig. 3, *d*). The lower portion of the fused sperm sacs (*s.c.*) occupies most of this space ; the upper portion of the sperm sacs lies *behind* the projecting posterior shelf of the anterior triangular shield (Fig. 3, *a'*—see also p. 240). In Fig. 3 the spermatophores and the entire right half of the dorsal wall of the pouch have been removed to expose the continuation of the triangular shield.



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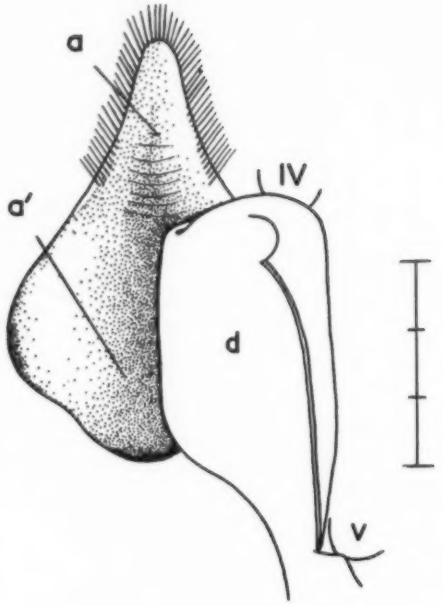

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Fig. 2.—*Penaeus japonicus* Bate. Thelycum of female represented in Fig. 1, dissected. Ventral wall of pouch removed to show the spermatophores in position. *a*. Anterior portion of the triangular shield of seventh thoracic sternite. *d*. Right half of dorsal wall of the pouch. *r*. Yellow rod. *s.c*. Median posterior portion of fused sperm sacs. *st*. The remaining proximal part of the stoppers. IV and V. Bases of peraeropods IV and V respectively.

Fig. 3.—*Penaeus japonicus* Bate. Thelycum of female represented in Fig. 1, dissected. Right half of dorsal wall of pouch removed to show the posterior shelf-like prolongation (d) of the anterior triangular shield. (Scale=3 mm.). Other lettering as in Fig. 2.

The median part of the exposed shield is moderately concave and the lateral part is slightly inflated. Moreover, while the triangular anterior portion (*a*) is firmly attached, the posterior part (*a'*) is free and forms part of the ventral wall of the seminal receptacle (*cf.* Fig. 10, *a'*). The greater part of this plate-like structure, therefore, is concealed by the pouch which, moreover, is not as simple as may appear at first sight. In order to understand it completely it is necessary to follow the development of the thelycum in detail.

DEVELOPMENT OF THE THELYCUM

The youngest female at my disposal is about 75 mm. long (tip of the rostrum and of the telson broken, carapace : 21 mm.*). The thelycum (Fig. 4) at this stage has little or no resemblance to that of an adult. On the seventh thoracic sternite there is a large triangular protuberance ; its central portion is modified to form a markedly concave shield (*a*) with raised setose lateral margins. On the eighth thoracic sternite there is a U-shaped plate, (*b*), which will eventually become the pouch, arising from the anterior border of a thickened transverse ridge (*c*).

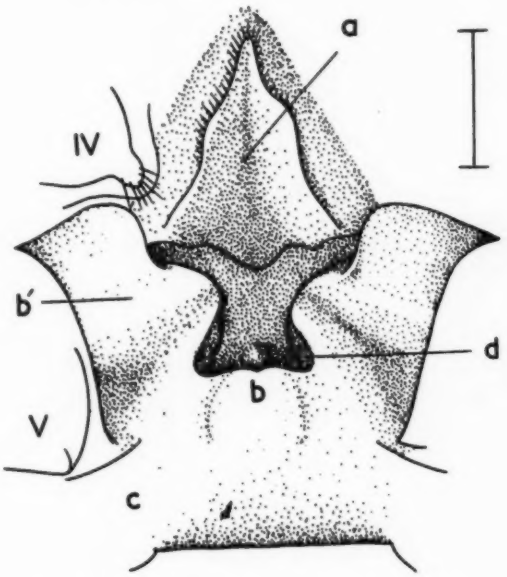


Fig. 4.—*Penaeus japonicus* Bate. Early stage in formation of the thelycum (female from Bay of Bengal, carapace length=21 mm.). *a*. Shield on anterior triangular protuberance. *b*. Incipient ventral wall of pouch. *b'*. Lateral arm of U-shaped plate. *c*. Transverse ridge. *d*. Incipient dorsal wall of pouch. (Scale=1 mm.).

Kubo (1949, p. 130, Fig. 57, A, B, C) has figured earlier stages in which the anterior margin of the ridge *c* can be clearly seen. The posterior margin

* The carapacial-length is determined by measuring from the post-orbital border to the posterior dorsal border.

removed to show the posterior shelf-like prolongation (*d*) of the anterior triangular shield. (Scale=3 mm.). Other lettering as in Fig. 2.

of ridge *c* is, I assume, the posterior limit of the eighth thoracic sternite. For the sake of convenience the U-shaped plate may be divided into three portions, two lateral wings (b′) and a median part (the plate *b*) the future ventral wall of the pouch. Most of the U-shaped plate and the ridge *c* are firmly fused to the body wall ; the sinuous anterior margin—behind the base of the triangular shield *a*—is free and slightly raised thus enclosing a median depression which extends beneath the anterior portion of the part indicated as *b* in Fig. 4. Posterior to the inner (median) bulge on b′ the margin tends to get tucked under *b* ; these infoldings (*d*) are the future dorsal walls of the pouch (*c.f.* Fig. 2). Just in front of *b* there is a small spine ; according to Kubo (1949, p. 129) the thelycum in a very early stage of development is represented simply by a median sternal spine on each of the two posterior thoracic segments. Later on the spine of the seventh segment takes part in the formation of the triangular plate *a* whereas that on the eighth segment disappears. At the stage represented in Fig. 4, the spine on the last thoracic segment is present but reduced in size.

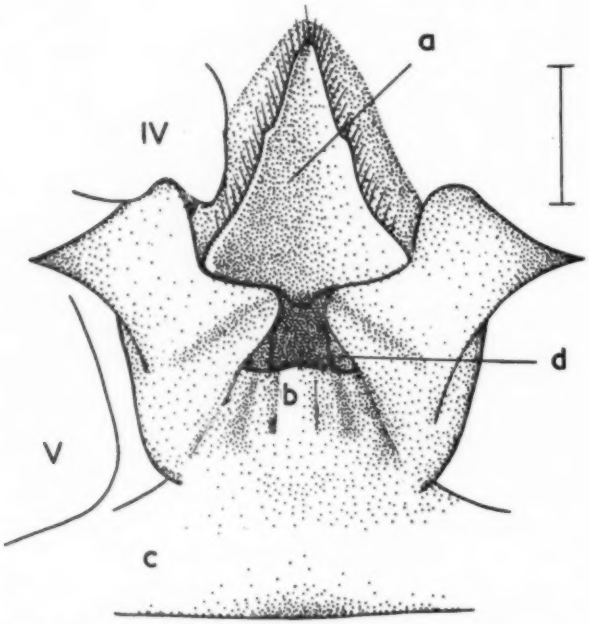


Fig. 5.—*Penaeus japonicus* Bate. Later stage in formation of the thelycum (female from Bay of Bengal, carapace length = 24 mm.). *a*. Shield on anterior triangular protuberance. *b*. Incipient ventral wall of pouch. *c*. Transverse ridge. *d*. Incipient dorsal wall of pouch. (Scale = 1 mm.).

As growth proceeds, the lateral ridges of plate *a* become more prominent and setose (Fig. 5) ; the posterior margin gradually extends backwards until it forms the large shelf or ledge (represented in Fig. 3, *a*′). This ledge is free

from the body wall but dorsal to the pouch, as already mentioned. On the other hand the U-shaped plate undergoes remarkable changes. In a specimen measuring approximately 90 mm. in length (rostrum broken, carapace : 24 mm.) the beginning of the pouchlike appearance is apparent. The infolded portions (*d*) of the lateral wings extend nearer to the mid-line thus raising the median plate (*b*) which, moreover, extends further forward.

In a female measuring approximately 135 mm. (rostrum broken anterior to the inferior tooth, carapace : 31 mm.) the thelycum has almost assumed the form characteristic of the adult, as represented in Fig. 6. The infolded

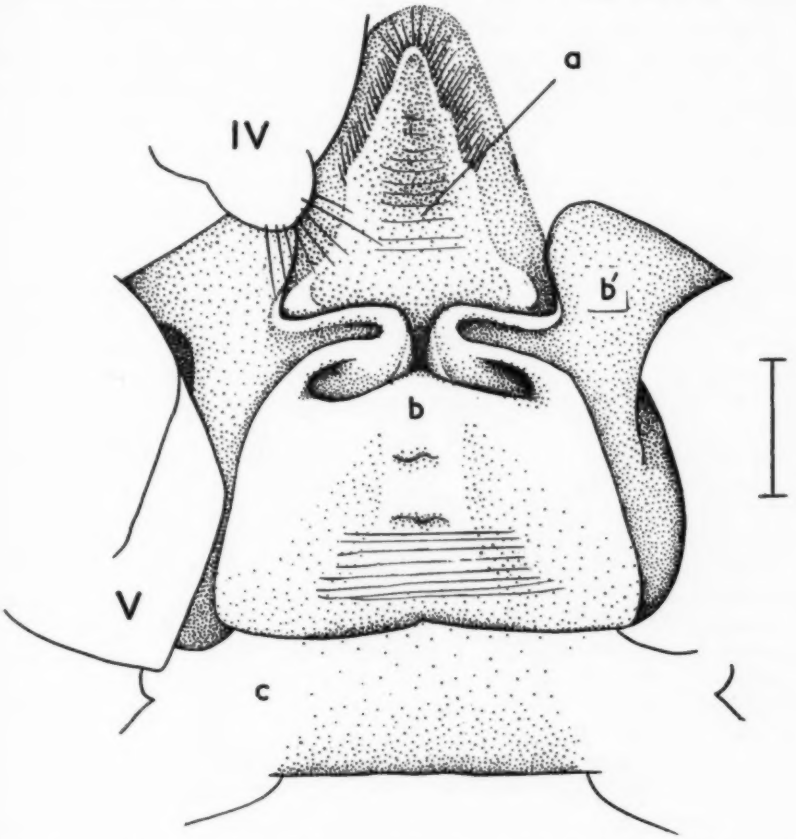


Fig. 6.—*Penaeus japonicus* Bate. Thelycum of the characteristic form, but not fully grown (female from Arabian Sea, carapace length=31 mm.). *a*. Shield on anterior triangular protuberance. *b*. Ventral wall of pouch. *b'*. Lateral arm of U-shaped plate. *c*. Transverse ridge. (Scale=1 mm.).

parts almost meet in the middle line ; each forms a double dorsal wall to the pouch and has grown forwards so as to conceal the posterior part of the triangular shield *a*. The soft ventral wall now occupies most of the space

between the bases of the peraeopods V although its anterior margin is less advanced than in the adult (compare Figs. 1 and 6). At this stage the dorsal layer of the infold is more advanced than the ventral layer, which in turn is more advanced than the anterior margin of the ventral wall (*b*) of the pouch.

In the fully grown female (Fig. 1), however, the whole pouch has extended forwards to reach the bases of peraeopods IV. The dorsal layer of the infold is no longer visible, being concealed by an antero-lateral extension of the ventral layer, and less than half of the anterior shield *a* is exposed. With the exception of the extreme lateral parts and the posterior margin of the ridge *c*, the whole pouch is now quite raised (protruding). The extreme lateral portions are hidden by the bases of peraeopods IV and V.

It is of importance to know that the cavity of the thelycum does not extend only as far as the bases of peraeopods V but goes further back to the posterior limit of the eighth thoracic sternite.

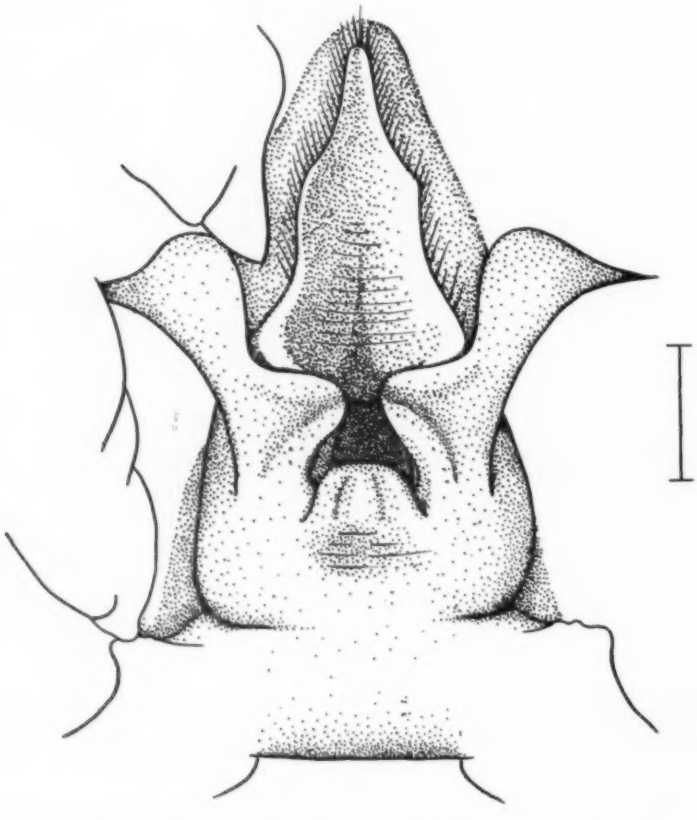


Fig. 7 —*Penaeus japonicus* Bate. Anomalous or retarded thelycum of a female from Arabian Sea, carapace length=27 mm. (Scale=1 mm.).

One female specimen in my collection is rather unusual in that, although the total body length is about 115 mm. (tip of the telson broken, carapace : 27 mm.), the thelycum is still at a comparatively early stage of development (Fig. 7). According to its size the specimen ought to have a well-formed thelycum but, as shown in the figure, the thelycum actually corresponds to that of a female with carapace length between 21 and 24 mm. Too little is known about the development of the secondary sexual characters in penaeids to enable us to understand this anomaly, which may only be a case of delayed or arrested development. However, it is of interest to note that, according to the stages of the Japanese population described by Kubo, in a female measuring 73 mm. (total length) the thelycum has already assumed the characteristic adult shape (1949, p. 130, Fig. 57, E) ; that of a female measuring 95 mm. has the typical thelycum though not quite fully grown (*c.f.* Fig. 6 of the present paper). According to Barnard (1950, p. 591), the latter condition is attained in South African specimens at a length of 85–90 mm. It would be necessary to examine much more material to ascertain whether or not these differences are geographical or seasonal.

THE SPERMATOPHORES AND THEIR RELATION TO THE THELYCUM

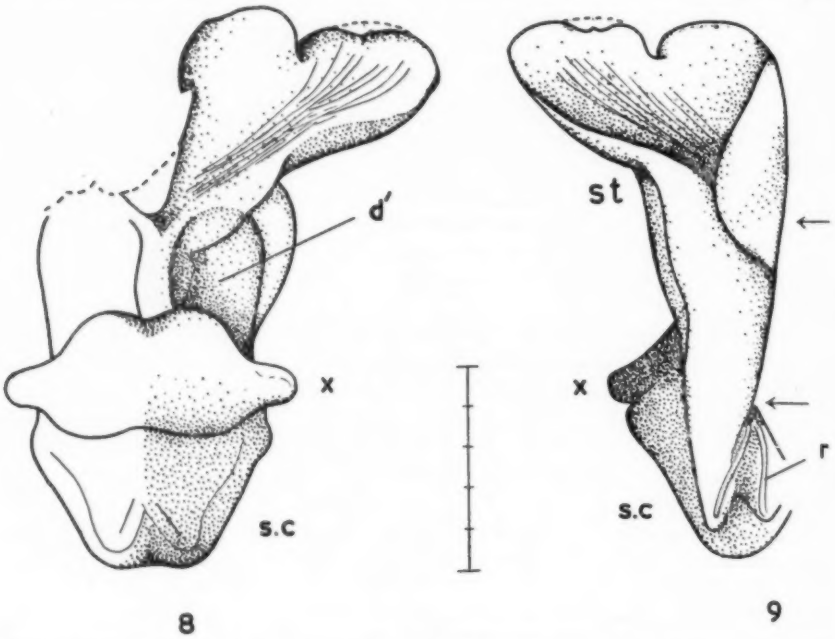
The complete spermatophores which are described below and represented in Figs. 8 and 9 were dissected from an impregnated female preserved in the Paris Museum. The details shown in Figs. 10 and 11 were obtained from the female from which Figs. 1–3 were made. Since the spermatophores of this species have never been fully described, I take this opportunity to do so in some detail.

Two symmetrical spermatophores are deposited in the thelycum ; these fuse along the median borders either at the time of copulation or later on. The fused spermatophores are represented in dorsal aspect in Fig. 8. A single spermatophore is shown in ventral aspect in Fig. 9 (the term dorsal and ventral are here used in relation to their position in the thelycum). It consists of a large wing-like portion (*st*), the stopper, and a shorter portion the sperm sac (*s. c.*), attached to the stopper only near its base. The spermatophore in lateral aspect resembles a hook. The distal part of the stopper, as shown in Fig. 9, resembles an expanded concave rather wrinkled leaf which appears to fold or curl over (opposite *st*) and which tapers to a point proximally. The stoppers are partially fused together along the median margin (between the two arrows) and, between the divergent bases, are two slender rods (*r*) which, in preserved material, are yellow. A small part of the sperm sac is visible in ventral aspect beyond the shaft of the stopper (Fig. 9, *s.c.*).

On the dorsal surface of each stopper is a depression made by the dorsal wall of the pouch of the thelycum (Fig. 8, *d'*). The two sperm sacs are firmly stuck (glued) together along their median surface. The general outline of the fused sacs is very similar to that figured for *Penaeus trisulcatus* Leach by Heldt (1938, Fig. 31). The anterior portion is slightly convex from side to side but markedly convex antero-posteriorly ; on either side there is a rounded lobular projection (Fig. 8, *x*).

Further details of the spermatophores were obtained by dissection of the

impregnated female from which Figs. 1 and 2 were drawn. In this instance most of the stoppers were, as already stated, missing. The right dorsal wall of the pouch was pulled away; while searching for the membranous wall of the seminal receptacle, which according to Hudinaga should be present, I inadvertently removed most of the sperm sacs. Then I pulled the right margin of the anterior triangular shield towards the left, in order to obtain Fig. 10.

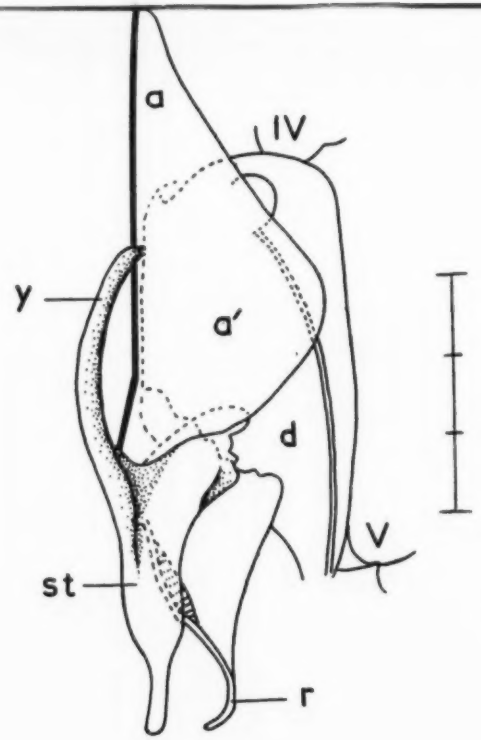


Penaeus japonicus Bate. Spermatophores dissected from thelycum of an impregnated female from Suez in Paris Museum.

Fig. 8.—Spermatophores in dorsal aspect, left one incomplete.

Fig. 9.—Right spermatophore of the pair shown in Fig. 8, in ventral aspect. *d'*. Impression made by dorsal wall of pouch of thelycum. *r*. Yellow rod. *s.c.* Sperm sac. *st*. Stopper. *x*. Lobe on anterior half of sperm sac. (Scale=5 mm.).

A curved rod (*y*) is seen attached to the dorsal wall of the sperm sac. It is difficult to say whether this is a continuation of the combined rods *r* (visible externally in ventral aspect as shown in Fig. 9), or an outgrowth from the stoppers, or a fused product of both rods and stoppers. This point requires further study as, unfortunately, my material is inadequate. The apex of the curved rod (*y*) bears two, perhaps three, spines which seem to pierce the anterior plate and thereby hold the sperm sacs in position. The position of the sperm sacs therefore is behind (dorsal to) both the dorsal wall of the thelycum and the anterior plate or shield (*a'*). The dorsal walls are not joined to each other and so, if the sperm sacs were merely pushed behind them, they would probably not stay in place.



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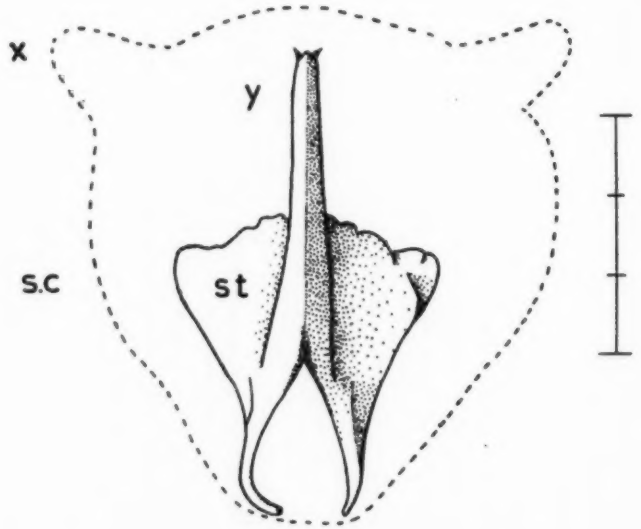

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Fig. 10.—*Penaeus japonicus* Bate. Thelycum of impregnated female represented in Fig. 1, dissected, and anterior shield pulled to left, to show position of spermatophores (sperm sacs removed). *a*, *a'*. Anterior triangular shield. *d*. Dorsal wall of the pouch. *r*. Yellow rod. *st*. Stoppers. *y*. Curved rod. (Scale=3 mm.).

Fig. 11.—*Penaeus japonicus* Bate. Stoppers (*st*) with the curved rod (*y*) dissected out from thelycum of female represented in Fig. 1, in dorsal aspect. The position of the sperm sacs (*s.c.*) is indicated by broken line. *x*. Lobe on anterior half of sperm sac. (Scale=3 mm.).

I dissected out the remaining proximal portions of the stoppers to which the curved rod *y* is attached (or of which it is an outgrowth). They are represented in dorsal aspect in Fig. 11 ; the outline of the fused sperm sacs is indicated by a broken line.

DISCUSSION

In order to discuss the development of the thelycum of *P. japonicus*, it is necessary to know its relation to the thelyca of some other species of the genus *Penaeus*. As mentioned above, Kubo has made an extensive study of the thelycum in many Japanese and other species of the family Penaeidae. As a result of this comparative study he divided the family into eight super-specific groups, according to the types of the thelyca that occur. He placed *P. japonicus*, along with other Indo-Pacific species of *Penaeus* and one Pacific American species *P. brevirostris*, in a group which he called " Type N_8 ". This type he defined (on p. 115) as follows : " Sternite of the last thoracic segment has anteriorly a median process and posteriorly a large seminal receptable. Anterior process is situated on sternite between fourth pereiopods, embossed with an apical protuberance which is variable in outline. Seminal receptacle occupies most part of the last thoracic sternite, is usually composed of two lateral plates which come into contact with each other along median borders, and somewhat overlap anterior median process by its antero-median margins, and rarely cylindrical with entrance anteriorly. Posterior border of eighth thoracic sternite has no median protuberance (Fig. 49) ". Further, he observed that " the seminal receptacle is cylindrical in *P. japonicus* only ".

The formation of a pouch-like structure in the case of *P. japonicus*, instead of two lateral plates on the eighth thoracic sternite, was suggested by Burkenroad (1934, p. 89) to be either due to " . . . the median fusion of the lateral plates or, more probably, the shifting forward of the posterior margin of the U-shaped elevation, . . . ". Kubo (p. 132) on the basis of his investigations supported the second alternative *i.e.* " the shifting forward of the posterior margin of the U-shaped elevation ". It seems that no importance was attached to that part of the thelycum which in the present papers is described as b′ (Fig. 4). Moreover, Kubo did not show how the dorsal wall of the pouch is formed ; this, as we have seen, is the result of the infolding of the lateral arms. The formation of the pouch-like structure from the original U-shaped plate is a complicated process involving folding, tucking in and anterior growth of the plate.

This peculiar structure of the pouch seems to be of great advantage at the time of copulation. If a transverse section be taken near the median line of big the pouch, four layers will be seen—the ventral wall, double dorsal walls and the anterior plate *a′* (Figs. 3 and 10)—lying one on top of the other. When the big spermatophores are inserted into the pouch through the anterior transverse opening, the cavity of the pouch can be greatly enlarged, and the broad anterior portion of the sperm sacs pushed through the arc-shaped opening (Fig. 2) behind the dorsal walls, and secured in position behind the anterior plate *a′*.

Heldt has described and figured the structure of the spermatophores in *Penaeus trisulcatus* Leach, *Parapenaeus longirostris* Lucas and *Solenocera*

membranacea H. M.–Edwards. The spermatophore differs markedly in these three species, belonging to different genera, and, as might be expected, that of *Penaeus japonicus* is nearest to that of *P. trisulcatus* (Heldt, 1938, p. 47, Fig. 7 (2)). However, in the latter species, the sperm sac is enormous and bears two wing-like membranes. As far as I can judge, the large foliaceous membrane (L.) of *P. trisulcatus* corresponds to the stopper (*st.*) of *P. japonicus*, and the narrow membrane (*l*) probably corresponds to the curved rod (*y*) and the yellow rod (*r*)—*c.f.* Figs. 8 to 11 of this paper with Heldt's figure quoted above. In *P. japonicus* the yellow rod probably gives support to the sperm sac ; it is also highly probable that the two yellow rods fuse or adhere (Fig. 2) and are continued as the curved rod *y* (Figs. 10 and 11) which, besides giving support, also helps in securing the sperm sacs within the thelycum.

The egress of the sperms from the sperm sacs at the time of spawning in *P. japonicus* has been stated by Hudinaga (1942, p. 314) to be through a pair of very tiny apertures of the seminal receptacle located at the bases of paraeopods IV of the female. But the present study, based on the structure of the sperm sacs and their position in the thelycum, supports Heldt's (1931) observations in *Penaeus caramote* Risso. In both species the females are soft at the time of copulation. Heldt says that after the introduction of the spermatophores the walls of the spermatophores unite intimately with those of the thelycum of which all the openings are obliterated with the exception of two small orifices towards the bases of peraeopods IV. The splitting open of the spermatophores takes place not far from these orifices. Further she says that the numerous hairs of the thelycum and of peraeopods IV direct the sperms forwards towards the bases of the third pair. It would seem, therefore, that the sperm sacs burst open at the two knob-like projections *x* (Figs. 8, 9, 11) which lie very near to the bases of peraeopods IV and the sperms are then directed forwards by the aid of the hairs on the anterior plate (*a*) as well as those on the coxae of the fourth pair of legs. In my material the small openings demonstrated by Hudinaga could not be found and indeed there seems no need for them. Burkenroad (1934, p. 89) has also, in the case of *Penaeus brasiliensis* Latreille, supported Heldt's observations on the egress of sperms from the disintegrated spermatophores.

SUMMARY

1. The thelycum of *P. japonicus* Bate consists of two parts (i) an interior triangular plate, and (ii) a posterior pouch.

2. The formation of the pouch is described. It is a complicated process involving folding and tucking in of the lateral arms of the U-shaped plate and anterior growth, notably of the transverse median portion of this plate.

3. The structure of the spermatophores is described, and their relation to the thelycum in an impregnated female. This description supports Heldt's work on *Penaeus trisulcatus* Leach.

ACKNOWLEDGMENTS.

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THE BEHAVIOUR OF THE GIRAFFE, *GIRAFFA CAMELOPARDALIS*, IN THE EASTERN TRANSVAAL

BY

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Toronto, Ontario, Canada

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(With 1 plate and 6 figures in the text)

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INTRODUCTION

Little precise information has been published about the habits of the giraffe. The structure of the herd in this mammal is unusual because the giraffe is one of the few ungulates that breeds throughout the year.

The results of the research on the behaviour of the giraffe reported in this paper are the outcome of a continuous field study extending over eight months. The work was done in South Africa from September 1956 to May 1957 on the Fleur de Lys farm in the Eastern Transvaal.

RESEARCH AREA

Transvaal Lowveld

In the Union of South Africa the giraffes are found only in the Transvaal Lowveld between Mocambique and the Drakensburgs, and between the Crocodile and the Letaba Rivers. Inside the Kruger National Park they are largely present south of the mopani tree belt which extends north of the Oliphants River. Outside the Park, they are found between the Oliphants and the Sand Rivers, although only outside the Native Reserve which begins south of Fleur de Lys farm. They are most plentiful in the Klaserie Valley where this study was carried out. A few giraffes have been found as far north

as the Letaba River and one was recorded near Shingwedzi. Some have also been recorded recently south of the Sand River, and a few as far south as the Sabi River, east of the Native Reserve. See Figs. 1 and 2.

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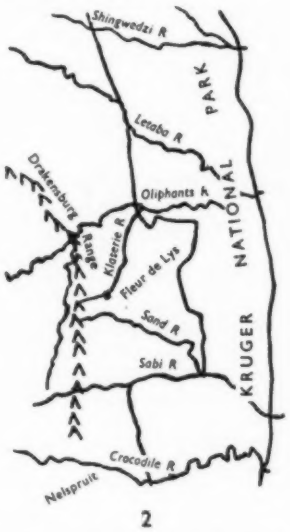

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Fig. 1.—Map of the Union of South Africa showing the Eastern Transvaal or Lowveld.
Fig. 2.—Map of the Eastern Transvaal or Lowveld.

In general, as browsers, giraffe have fewer mass migrations than most other kinds of game which are dependent on the veld itself. Even in times of drought the leaves of trees begin to grow in the spring although there may be no signs of new grass growth. Giraffe too are affected if the rivers dry up however, and when very dry springs occur giraffe and other game in the Klaserie area move up the river as the water stops running and the pools dry up farther east. To the west, away from the Kruger National Park the food is more abundant as rain is more general closer to the Drakensburg Range. The temperature range in this area is between 32 and 105 degrees Fahrenheit.

Klaserie area

Up until 1946 all the land east of the main Tzaneen-Nelspruit Road was largely unfenced and unfarmed so that game could wander freely from here to the Kruger National Park. However in 1946 the Guernsey Block was settled and much of the game in this area was shot or chased out when the farms were started. No giraffes were ever found west of the main road, probably because this area was being quite heavily farmed and was separated from the east of the main road by three fences and the Selati Railway Line. For a year or so after the extensive fencing on the east side in 1950, the giraffes in that area were continually breaking down the fences until they were in danger of being shot out as a menace to farming. Then this fence-breaking

suddenly became negligible and it was discovered that the giraffe had learned how to cross the fences, first by lifting the two front legs over separately and then hopping the hind legs over. After this, giraffes were occasionally seen west of the main road, as fences no longer served as a major obstacle.

Fleur de Lys Farm

On Fleur de Lys and Moriah farms there is an abundance of giraffes, the number remaining fairly constant in winter and summer but increasing in very dry seasons. In 1953 the native rangers estimated that there were a total of ninety-five giraffes and the number present in 1956–7 was probably much the same. The giraffes have adapted themselves rapidly to their new environment, jumping the fences readily and drinking at the cattle troughs, often stepping among the cattle to do so. Whereas formerly a herd could wander over vast distances, now a group will stay in one paddock for at least a year.

A map of the eastern halves of the two adjoining farms, Fleur de Lys and Moriah is given in Fig. 3. The western area of these two farms contained very few giraffe and has not been included in the study. The area included in Fig. 3 will be referred to simply as Fleur de Lys.

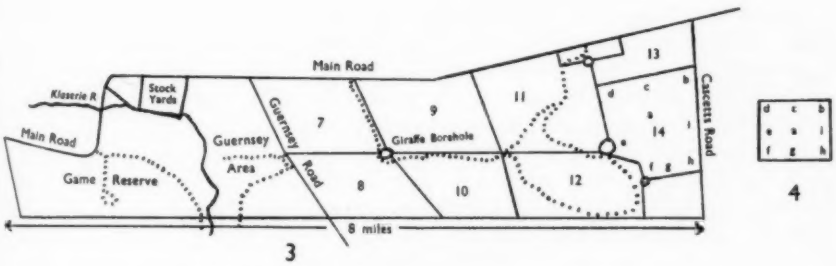

Fig. 3.—Map of the half of Fleur de Lys farm where the giraffe study was carried out.
———— Boundaries of fences.
. . . . . Tracks in the camps along which a car could drive.
Fig. 4.—Diagram showing the letters which indicate locations in the camps, as labelled in Camp 14 of Fig. 3.

VEGETATION

The vegetation of Fleur de Lys, which has an average rainfall of twenty-six inches per year, corresponds with that described by L. E. W. Codd in his book *The Trees and Shrubs of the Kruger National Park* as " large-leaved deciduous bush " and which is found around the Pretorius Kop area. At Fleur de Lys four types of vegetation occur—bush veld, parkland, thorn bush and open area composed entirely of grass.

Bush Veld

All the Camps numbered from 7 to 14 are covered with bush veld, with varying denseness of the bush in different local areas. To indicate the type and denseness of this bush, a quadrat study was carried out in an area of

medium dense bush chosen at random and situated in Camp 8d. It equalled 4364 square yards. Besides the grass which is invariably present under the bush, this area included the following plants :

Trees over 10 feet	No.	Plants under 10 feet	No.
Combretum suluense	16	Combretum gueinzii	5
Terminalia sericea	3	Acacia swazica	60
Dombeya rotundifolia	4	Acacia suberiana	2
Dalbergia melanoxylon	3	Acacia grandicornuta	2
Sclerocarya caffra	1	Heeria reticulata	2
Ziziphus mucronata	1	Dicrostachys nyassana	2
	—	Euclea lanceolata	1
	28	Acacia burkei	1
		Grewia flavescens	1
			—
			76

Therefore three-quarters of the plants present were under ten feet tall, and there were 104 plants in 4364 sq. yds. The density was one plant for every 42 sq. yds. In different areas the variations on such a result will be practically infinite.

In the southern area of the farm, marked Guernsey Area and Game Reserve on the map, conditions were different. A large part of this area was heavily cultivated by Africans up to 1949–50. At that time erosion was very bad. Much of the area is now bare of bushes and only a few trees may be found scattered on the open fields of grass. These open areas are varied by small areas covered with thorn bush. In the valley of the Klaserie River and bordering the dongas, dense bush is again found of the same type as described above.

Random quadrat studies of Parkland and Thorn Bush types of vegetation were made to show the type and denseness of the vegetation present. Here too, variations on each type are infinite and the results merely give a general indication of the conditions present.

Parkland

The trees listed below are the ones found within a seventy-five pace radius of a Marula tree chosen at random. The area equalled 11,599 sq. yds.

Trees	No.	
Sclerocarya caffra	7	
Trichilia emetica	7	
Lonchocarpus capassa	4	
Combretum imberbe	3	Other common parkland trees include :
Piliostigma thonningii	2	Terminalia sericea
Grewia flavescens	2	Schotia brachypetala
Euphorbia ingens	1	Diospyros mespiliformis
Euclea divinorum	1	Ficus petersii
Combretum suluense	1	Ficus sycomorus
Heeria reticulata	1	Acacia giraffa
Acacia sp. bushes	4	
Combretum gueinzii bushes	4	
Strychnos dysophylla	1	

In the 11,599 sq. yd. area there were thirty trees over ten feet tall. The density therefore was one tree per 1·273 sq. yds.

Thorn Bush Area

The random area chosen was 98·4 sq. yds. The bushes were all under ten feet tall and included :

Bushes	No.
Acacia swazica	22
Ziziphus mucronata	1
Ormocarpum trichocarpum	9
Dicrostachys nyassana	1
	33

There were thirty-three thorn bushes in 98·4 sq. yds., or a density of one bush for every three sq. yds.

Open Area—Guernsey and Game Reserve Area

This area was more open then the rest and so the movements of the giraffes inhabiting it could be more carefully observed. An intensive study was therefore carried out here, and a vegetation map is included with the tracks marked along which a car could travel. The land is undulating, the dongas and denser growth indicating valleys and the open grassy areas usually on higher land. (Fig. 5).

FOOD

To discover what food giraffes eat, it was necessary to watch them from a car, which could park within fifteen yards of a browsing giraffe without disturbing it unduly. If a food plant was unknown, a yellow ribbon was tied around the tree or shrub so that a branch could be collected later for identification. The specimens were kindly identified by the Government Division of Botany in Pretoria.

A list of the food plants of the giraffe was made from observations taken in September and October, at the end of the dry season. During this time, their diet would presumably be as varied as at any period because only comparatively small amounts of leaves and buds are available on each tree.

The September and October food plants included :

Acacia burkei Benth. +
Acacia grandicornuta Gerstner. +
Acacia robusta Burch. +
Acacia suberiana D.C. +
Acacia swazica Burtt Davy. +
Albizzia harveyi Fourn. +
Balanites Maughamii Sprague. Torchwood
Cassia petersiana Bolle. +
Combretum apiculatum Sond.
Combretum gueinzii Sond.
Combretum imberbe Wawra. Leadwood
Combretum suluense Engl. & Diels.
Dalbergia melanoxylon Guill. et Perr + Zebra-wood
Dichrostachys nyassana Taub. + Sickle-bush
Dombeya rotundifolia (Hochst.) Planch. Wild pear
Euclea divinorum Hiern.
Ficus petersii Warb. Peter's wild fig
Ficus sycomorus L. Sycomore fig
Grewia sp. aff. flavescens Juss.
Gymnosporia senegalensis (Lam.) Loes.
Heeria reticulata Engl.
Lonchocarpus capassa Rolfe +
Mundulea sericea (Willd.) +
Ormocarpus trichocarpum (Taub.) Harms. +
Piliostigma thonningii (Schum.) Milne-Redhead +
Pterocarpus angolensis D.C. + Kiaat
Pterocarpus rotundifolius (Sond.) Druce +
Sclerocarya caffra Sond. Marula
Strychnos dysophylla Benth. Monkey orange
Strychnos spinosa Lam.
Terminalia sericea Burch.
Ziziphus mucronata Willd. Buffalo-thorn

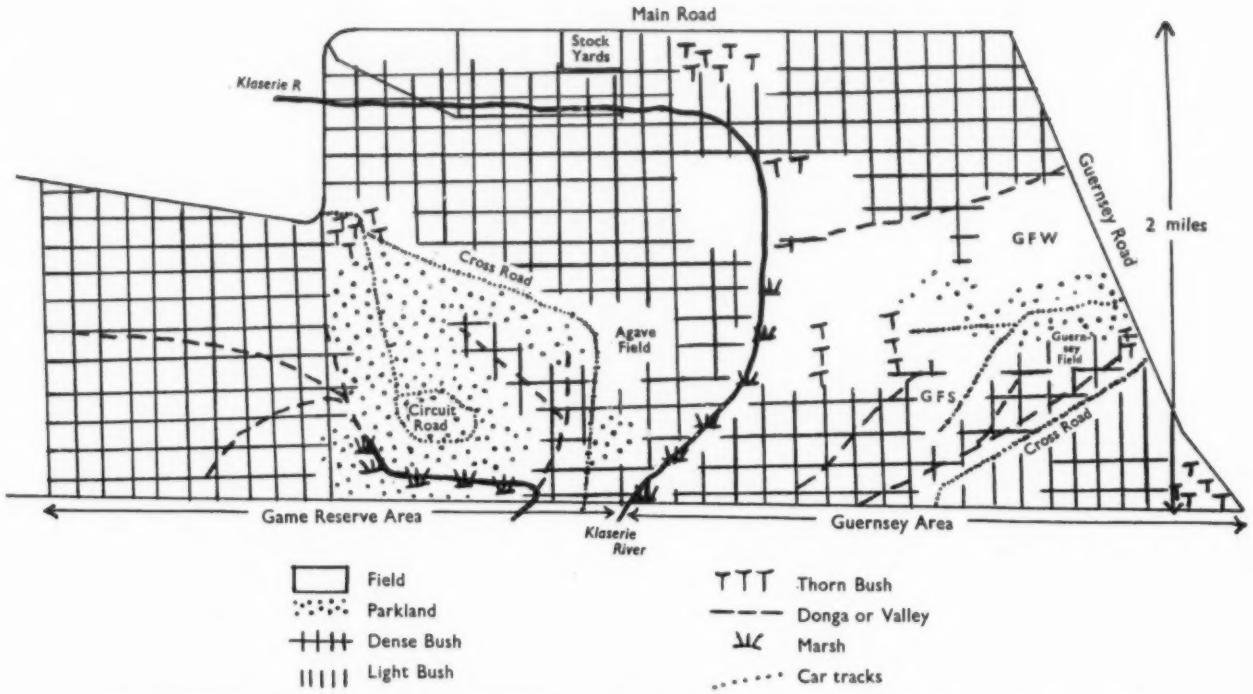

Fig. 5.—Map of the Game Reserve Area and the Guernsey Area where an extensive study of the giraffe was carried out.

It is interesting to note that a large number of these plants belong to the family Leguminoseae (those marked with a +), and that many of these plants have thorns.

In December, when all the trees are in full leaf, the giraffe feed more selectively. To ascertain the plants giraffe prefer under these conditions, a record was kept of the number of times a giraffe was seen eating at each different type of tree or bush. All these observations were taken during the month of December from all parts of the farm to eliminate errors arising from studying a small area with limited trees, or only a few giraffe. The results are not large enough to indicate more than a general trend.

List of plants and the number of times each was seen being eaten.

Lonchocarpus capassa	19	Pterocarpus rotundifolius	3
Terminalia sericea	18	Unknown	3
Dalbergia melanoxylon	8	Dicrostachys nyassana	2
Acacia swazica	8	Piliostigma thonningii	2
Combretum apiculatum	6	Pterocarpus angolensis	2
Combretum gueinzii	6	Cassia petersiana	1
Albizzia harveyii	5	Combretum imberbe	1
Ziziphus mucronata	4		

From these observations it is evident that the diet of the giraffe is still very varied at this time of year.

The trees are in full leaf in December and it is easy to see from which trees giraffe have eaten, as these have few or no leaves up to a height of about sixteen feet, and full foliage above that point where giraffe cannot reach. (Plate 1). Several specimens of all the main types of trees in the Guernsey Area were examined and the proportion of foliage removed noted. This information serves to implement the above results where no account is made of the leaves of trees having been so thoroughly eaten previously that there was little left for the giraffe to browse on in December. This was true of *Combretum imberbe*.

Proportion of foliage within Giraffe-reach eaten from trees in December :

Ficus sycomorus	large	Balanites Maughamii	small
Ficus petersii	large	Albizzia harveyii	small
Combretum imberbe	large	Sclerocarya caffra	very small
Combretum apiculatum	large	Heeria reticulata	none
Terminalia sericea	large to medium	Dombeya rotundifolia	none
Strychnos dysophylla	medium	Combretum suluense	none
Ziziphus mucronata	medium	Trichilia emetica	none

It is interesting that all but *Trichilia* of the last five species were well browsed in September and October when food was scarce, but were nearly untouched in December when giraffes have a wider choice and when the leaves are no longer as young and succulent. During December, a giraffe was observed licking the rusty metal bars of a gate which may indicate some mineral deficiency in his diet.

Few leaves had fallen from the trees in early May, but the leaves were usually old and would therefore be less nutritious. At least five of most of the species of trees on the farm were studied, and the proportion of foliage eaten by giraffes noted.

Proportion of foliage gone from trees in May, owing to feeding by giraffes :

Combretum imberbe	all	Combretum transvaalense	very little
Cassia abbreviata	all	Pterocarpus rotundifolius	none (little)
Pterocarpus angolensis	all	Heeria reticulata	none
Strychnos dysophylla	all	Dombeya rotundifolia	none
Strychnos spinosa	all	Cassia petersiana	none
Acacia nigrescens	all (most)	Piliostigma thonningii	none
Ziziphus mucronata	all to most	Schotia brachypetala	none
Ficus petersii	all to most	Diospyros mespiliformis	none
Dalbergia melanoxylon	most to some	Balanites Maughamii	none
Acacia swazica	most to some	Combretum suluense	none
Combretum apiculatum	some	Euclea divinorum	none
Combretum gueinzii	some	Lonchocarpus capassa	none (old (leaves)
Terminalia sericea	some to none		
Sclerocarya caffra	some to none	Ficus sp. (1 tree)	none

In winter the trees are bare, and the giraffe subsist on twigs.

Chemical analyses are being carried out on dried leaves collected in September, December and May from species of trees on which giraffe feed and on those on which they do not feed. This study it is hoped will show why giraffes eat certain leaves and whether their choice is based on the chemical composition of the leaves or on their taste, or on neither of these characters.

As a further seasonal study, giraffe droppings were collected monthly and are now being analysed chemically to see if less fibrous matter from twigs and the less nourishing foods is present later in the season, as would be expected.

INDIVIDUAL ACTIVITIES

When observing giraffe seven × fifty binoculars were used.

Feeding

How and why the giraffe selects certain plants to browse on is interesting. Sight and smell both seem to play their part. It is quite common to see a giraffe walking along and looking at the bushes until coming to a suitable bush at which to stop and browse. One female walked thirty yards across a grassy patch to feed at a small isolated thorn bush in the field. The sense of smell is often a deciding factor as I have seen a giraffe sniff at a bush before starting to feed at it. It must be particularly valuable at night when giraffe have been seen eating avidly although it was so dark that only their silhouettes were visible.

Trial and error may also be important, because I have seen a female eating at five different bushes in succession, taking no more than six bites at each. Two males were timed for five minutes while feeding and in that time one browsed at four bushes, three of them within the last minute. The other male fed only at one bush and did not pause or look up during the five minutes.

Giraffe begin browsing when very young and one baby was seen feeding at a thorn bush when it could not have been more than one or two weeks old. It was interesting to see all the taller giraffes feeding at one favourite tree whose lower branches had been eaten away, while the smaller giraffes who could not reach the foliage fed at shrubs nearby.

At times, feeding seems to serve as a displacement reaction. I once drove right up to a large old bull giraffe which retreated about twenty yards from the track. As he turned to face the track again, his head touched a branch of leaves and he nibbled at one for a second before staring motionless at the car for five minutes. In another instance, a male in the middle of a serious head-hitting battle with another male had his head bent down after a lunge, and he suddenly took a few bites from a bush near his nose before continuing to exchange blows with his opponent. I have also seen a giraffe chewing his cud suddenly stop and eat a few leaves before starting to chew again.

A giraffe does not bite off twigs or leaves when feeding, but tends to take a branch in its mouth and then pull its head away so that the leaves are torn off in its mouth. It even browses from thorn bushes in this way, its thick bristly prehensile lips protecting it against wounds from the thorns. The tongue, eighteen inches long and both tactile and prehensile, serves a useful purpose in feeding.

Drinking

Giraffe have been seen drinking at the cattle trough or at the water pit at all hours of the day and even as late as 8 p.m. when it was dark. At times the giraffe seem very nervous, some or all the animals in a herd preferring not to drink if natives or a car are in the vicinity of the water, so that they may return to the bush without drinking at all. At other times, they are remarkably incautious and I have watched a herd of six giraffe drink at a waterhole when my car was parked only thirty yards away from them. I have also seen them drink at the cattle trough when African men with whips were rounding up a large herd of cattle eighty yards away at the adjoining trough.

When they drink, they reach the water by straddling their forelegs sideways or by bending their front knees forward. They often drink for twenty seconds at a time and when finished straighten up again very quickly. They may bend down as many as six times, possibly because it is tiring for them to remain bent down for too long at a time.

Chewing

Giraffe chew their cud at any time throughout the day, when walking, standing or lying and between spells of browsing. Often all the giraffe in a herd will stand or lie in one place for hours, patiently chewing.

A female giraffe was timed while she chewed seven cuds. The highest number of chews per cud was forty-nine, the lowest twenty-nine and the average forty-four chews per cud. Each chewing motion took an average of 0·94 seconds. A chew per second seems to be about normal, as two other giraffes took 0·98 and 1·0 seconds per chew respectively.

Standing

Giraffe are often seen in the heat of the day just standing about, facing in different directions and not chewing. They seem to be drowsing, often with their heads lowered so that their necks are bent like a bow, and they move their tails infrequently.

Lying

As in most of their other habits, giraffe show individualism when lying down. They usually lie down about twenty yards away from each other and then rest, perhaps chewing their cud or even nibbling at a low bush, for from five minutes to over an hour. They lie either in the sun or in the shade and facing any direction, which cannot be oriented with the position of the sun or the way the wind is blowing. I have watched two lying down for one hour facing opposite directions, and in that time neither acted as a sentinel or looked anywhere but straight ahead. A giraffe will lie down or get up with little or no reference to what other giraffes are doing, and sometimes a giraffe will remain lying for twenty minutes after the rest of the herd has moved out of sight.

In daylight, they usually rest with their heads erect, but once I noticed one lying down with his neck stretched back beside his body and his head tucked back beside his tail for five minutes. This is assumed to be the position for real sleep. (Jones, 1956 and Grzimek, 1956).

When a giraffe is lying, the legs are either all tucked up to one side of the body, or else the forelegs are folded up underneath the body in the attitude of a sphinx. To lie down, they kneel with the forelegs first, and rise with the hind legs first.

Walking and Running

Giraffe have two gaits only, a rack-like walk with both legs on one side off the ground simultaneously, and a gallop. The long neck and head serve as an extra anterior weight and this weight distribution tends to throw them forwards so that they can afford to have two legs off the ground at one time, which permits a faster pace. When galloping, they bring their hind feet in advance of and to the outside of the forefeet, and the fore and hind legs on the same side move together. This unusual movement may be either an adaptation to height, or to the slanting character of the backbone of the giraffe.

The giraffe is extremely fast, with a speed of 35 m.p.h. over short distances (Bigalke, 1939) and one of 28–32 m.p.h. for several miles. (Maxwell, 1924). When galloping, the tail is twisted up over the back like a corkscrew, presumably to prevent it being caught on thorns.

Young giraffe sometimes run for no apparent reason, except perhaps an excess of energy, but the adults wait until danger is near. Otherwise they walk at a leisurely pace which becomes extremely slow in the heat of the day.

Rubbing

Ticks are very numerous in the Lowveld, and their numbers increase in the rainy season. The ticks tend to congregate under the stomach and around the genitalia of the giraffe where there is less hair. Although the hide of the giraffe is as much as one inch thick, the animals seem to be greatly bothered by

these ticks and were often seen rubbing themselves on anything convenient. To scratch the stomach, they would stand over a six foot bush and rock backwards and forwards. If the ticks cause the back to irritate they back slowly in and out of the bush. If a giraffe needed to scratch head or neck, it might do so by rubbing it on a tree, on the head or neck of another giraffe, or even on the ground. It can reach back and rub its foot or flank with its mouth. If the foot continued to itch, it might walk to a low bush and drag the leg backwards and forwards among the branches.

One female got something stuck in her nose. After sneezing several times she tried rubbing her head on her flank and eventually, still sneezing, she walked to a bush and rubbed her head in it.

Pawing the ground

This action was noticed many times. In each case the giraffe was staring at me, and while still staring stamped or pawed the ground with the forefoot as many as three times in close succession. These may have been threat reactions but the general attitude indicated that it was more probably a nervous reflex on the part of the giraffe.

Jumping fences

Only the bigger giraffes jump over the four foot six inch wire fences, and some individuals are more nimble than others. They lift the two forelegs over separately, move forward until the back legs touch the top wire, and then hop these two over together. Some get one of the back legs caught on the top wire and have to drag it over after them. One male paced along the fence until finding a hillock where the fence was lower, it jumped over at that point. Fences do act as a barrier however, if only psychologically. A female giraffe jumped over a fence with the other adults in a herd, and she left her baby on the other side of the fence. Both mother and baby paced along the fence opposite each other, but the mother would not jump over the fence again and the baby finally wandered away from the fence and was lost.

Head to the ground

On eight different occasions, giraffe were seen to spread-eagle their forelegs and put their head right down to the ground, as if either eating the earth or rubbing their nose or head. In several cases, one stretched down in the same place several times. In one such incident, I watched a male bend down three times in one place. When I walked to the spot he retreated and I could find nothing there but earth and a broken anthill, both of which seemed to be untouched. Game are known to use anthills as salt licks however (Hesse, 1955). When I went away the giraffe returned to the same spot and bent down a fourth time. In another instance a female spent most of one morning walking about in a grassy area and putting her head down at intervals as if looking for something. She did not quite touch the ground with her nose.

DAILY BEHAVIOUR

To find out how giraffe spend their time, a chart was kept in which every giraffe seen at each five minute interval was marked down as either feeding, standing and chewing, standing (resting), lying or fighting. Any giraffe which were walking or running when the five minute census was being taken were not counted. Records were kept for any giraffe that was seen at any time or place for as long as it was in sight. See Tables 1 and 2.

TABLE 1

Hourly tables of the total number of observations for each month and the percentage of observations for each activity.

	September						October					
		Percentage						Percentage				
	Total Obser.	Feed	Chew	Rest	Lie	Fight	Total Obser.	Feed	Chew	Rest	Lie	Fight
6– 7 a.m.	90	92	0	8	0	0	204	97	1	1	0	1
7– 8	130	78	1	15	0	5	333	81	5	3	2	10
8– 9	119	59	22	3	10	6	272	91	4	1	1	3
9–10	174	76	5	7	5	7	495	68	14	12	8	4
10–11	122	91	2	2	0	4	408	62	19	12	4	3
11–12	52	96	4	0	0	0	233	55	10	12	21	2
12–1 p.m.	78	69	3	27	0	1	15	47	7	0	27	20
1– 2	9	56	0	33	0	11	12	83	0	0	0	17
2– 3	46	65	11	0	22	2	33	64	12	6	18	0
3– 4	74	93	0	7	0	0	55	89	11	0	0	0
4– 5	54	100	0	0	0	0	96	100	0	0	0	0
5– 6	56	100	0	0	0	0	46	96	0	4	0	0
6–	2	100	0	0	0	0						
Total		1075	48	102	37	36		933	83	51	81	60
Percentage		83	4	8	3	3		77	7	4	7	5

	November						December					
		Percentage						Percentage				
	Total Obser.	Feed	Chew	Rest	Lie	Fight	Total Obser.	Feed	Chew	Rest	Lie	Fight
5– 6 a.m.	23	78	9	9	0	4						
6– 7	95	99	0	1	0	0	154	56	34	0	1	10
7– 8	124	52	19	10	19	1	140	58	38	4	1	0
8– 9	109	12	23	7	49	9	174	57	33	0	6	3
9–10	331	27	36	7	26	3	105	76	14	1	0	8
10–11	317	47	29	4	14	6	59	12	85	0·5	0	0·5
11–12	453	49	24	9	15	3	124	15	16	0	69	0
12– 1 p.m.	171	31	32	8	29	0	24	71	0	0	29	0
1– 2	134	31	11	13	45	1	19	68	0	0	32	0
2– 3	159	40	18	11	26	4	21	95	0	0	5	0
3– 4	119	72	14	6	0	8	42	93	4	2	0	0
4– 5	187	61	16	5	3	14	15	80	0	0	0	20
5– 6	31	77	10	0	0	13	31	90	6	0	0	3
6–	23	100	0	0	0	0						
Total		766	241	90	226	66		771	230	8	143	45
Percentage		55	17	6	16	5		65	19	1	12	4

TABLE 2

The percentage of time spent on each activity for every three-hour period

	September Percentage					October Percentage				
	Feed	Chew	Rest	Lie	Fight	Feed	Chew	Rest	Lie	Fight
– 9	76	8	9	3	4	90	3	2	1	5
9–12	88	4	3	2	4	62	14	12	11	3
12– 3	63	5	20	7	5	65	6	2	15	12
3–	98	0	2	0	0	95	4	1	0	0
Average percentage	83	4	8	3	3	77	7	4	7	5
	November					December				
– 9	60	13	9	17	5	57	35	1	3	4
9–12	41	30	7	18	4	34	38	0·5	12	3
12– 3	34	20	11	33	2	78	0	0	22	0
3–	78	10	3	1	9	88	3	1	0	8
Average percentage	55	17	6	16	5	65	19	1	12	4

Feeding

By far the greatest part of every day was spent in browsing. This proportion was highest in September and October when less food was available and more time had to be spent in finding the available food. Less time was spent this way in November and December when the trees were in full leaf. The favourite time for feeding was from 3 p.m. onwards, and then from early morning until 9 a.m. It is not known to what extent giraffe feed at night. From 9–12 a.m. was an important feeding time in September, but of decreasing importance as the season advanced, and can be regarded as a marginal browsing time used when food is scarce and less nutritious so that more time has to be spent in browsing.

Chewing

A progressively greater proportion of time was spent in chewing as the season advanced. As the giraffe needed less time to feed, they had more leisure to chew their cud in the daytime. Assuming that a given quantity of food requires a given amount of chewing, they also have more time to lie down during the day, which is what seems to happen. Of all the giraffe seen lying down, only one-third were chewing their cud.

In September, October and November chewing was spread throughout the day with the largest proportion from 9 to 12 a.m. but in December chewing occurred almost exclusively in the mornings followed by long periods of feeding in the afternoons.

Resting

The giraffe spent very little time resting, particularly after 3 p.m., and in December.

Lying

The highest proportion of giraffe seen lying down was observed in November and December rather than in September and October when more time was spent foraging for food. The greatest numbers were seen lying down between 12 a.m. and 3 p.m. in the hottest part of the day, and then between 9 and 12 a.m. Only one giraffe was ever seen lying down after 3 p.m.

Fighting

Fighting between the males occurred at all times of the day and in all the four month periods, as well as in April and May. This fighting between bulls must therefore be distinguished from the short fierce fighting that preceeds the breeding season of many species of antelope and deer.

In conclusion, browsing is the most time-consuming activity of the giraffe and is especially important in the morning and in the late afternoon. Less foraging was necessary in November and December when there was more food available, so that during these months the giraffe had more time to chew and to lie down. Fighting among the males is common and occurs throughout the day. It is not seasonal in nature.

SOCIAL ACTIVITIES

Courting

Courting behaviour in the giraffe was relatively rare—far rarer than mounting and sexual play among the males. The most common and distinctive phenomenom between sexes is that of urine testing, which occurs throughout the year. While a female is eating or chewing, a male often walks up to her and licks her tail, takes her tail between his lips, or merely lays his head on her flank. Without seeming to pay any attention, the female then urinates and the male collects some of the urine in his mouth or on his tongue. He then raises his head, closes his mouth, and curls back his lips in a very characteristic fashion, and several times I have seen one ejecting the urine from his mouth in a long thin stream. He may then lick his lips for a moment before beginning to chew or feed. One male may lean down and collect as many as three separate lots of urine from the urinating female. There is no jealousy among the males, for as many as three males may collect urine from one female at one time. In every case I have observed, the male payed no further attention to the female but moved off and began to feed or chew. In one instance a male licked a female's tail and then put his head up and stared at me while she urinated.

This behaviour has so far not been reported in any of the literature about the giraffe. Hediger (1957) says that the curling back of the lips after the male has nuzzled the urine of the female is found in many ungulates. Matthews (1957) says that the collection of urine by the male with the subsequent curling back of his lips occurs frequently among giraffe in captivity. I suggest that, as the hormone composition of the urine changes with the oestrous cycle, the male can test the urine of the female to see if she is coming into heat.

As well as testing a female's urine, a male will occasionally walk up to a female and sniff her tail lightly or rest his head gently for a moment on her

flank. Then he may move up and stand right behind the female as if intending to mount her. In every case but one, however, the female walked away and appeared completely uninterested. The one case was the only time I have seen giraffe mating. The male, which I will refer to as Star, mounted the female three times about 5 p.m. one evening, while a medium-sized bull stood close by and watched. The rest of the herd was not in sight. I was watching with field glasses from my car on the opposite slope about 400 yards away.

Star walked behind the female in an open area about twenty yards across surrounded by low bushes. Every time she came to the edge of the clearing Star hurried up beside her to head her back again into the clearing. This happened at least twice between each mounting. Star sometimes walked beside her and put his head down beside hers but she would move away from him. He followed her until she stood still facing downhill, and then stood behind her for a minute or so without either of them moving. He may have lightly kicked her hindlegs once with his forelegs. Then he mounted her by sliding his forelegs loosely onto her flanks and after a second or two she ran forward and he followed with his penis still erected for a short while. Then they walked around in a circle again until she stood still facing downhill. The medium-sized bull always stood to the front and the side of them and watched the mounting. After the third mounting, Star and the female were standing together when the medium male approached the female. Star walked around the female and towards this male who retreated a short way and then moved forward again. Star kept chasing him away and once he had to canter off when Star hurried up to him. A little later the medium male cantered right up to the female and she cantered beside him with Star walking behind them. Then they all cantered behind a dense bush and only the medium male emerged on the other side of the bush. Then Star appeared following the female and the other male tagged along behind them. Star had to keep chasing the medium male away as he was becoming more persistent and bold. Finally they all started to run at full speed up the hill, with Star heading the medium male off from behind the female. Then they all wheeled and ran downhill. The medium male soon overtook Star and ran up to the female while Star was left a little behind. Then they all disappeared into dense bush.

Homosexual behaviour in the giraffe will have to be placed between the sections on courting and fighting, as fighting in the males is very closely tied up with sexual behaviour and " necking ". " Necking ", or the gentle rubbing of one male's head or neck on another male's head, or along his neck or body, is very common and frequently arouses a male to the extent that he will stand behind and mount another or several males. Alternatively, after a male has mounted another male, they may begin to neck, and then spar lightly and then fight fiercely, with heavy blows from their heads taking the place of the gentle rubbing. Then they may suddenly stop fighting and one may mount the other again. Here again there is no jealousy. A male may stand behind another male with his penis erected, and before he can mount the other male he may walk away. With his penis still erected, the first male may then move up to another bull and mount him. Or again one male may mount another three separate times. In one case the mounting male kept his penis

erected. The male in front moved a few steps forward after having been mounted, and continued chewing, while the hind male sniffed at the other's tail, moved up behind him, and mounted him again. This mounting behaviour takes place throughout the year and often when there are female giraffe near.

The penis is about eight inches long, with a downwardly directed hook at the end, rather in the shape of a crochet hook. Liquid could sometimes be seen dropping in a very fine stream from the tip.

Homosexual behaviour is much more in evidence than heterosexual behaviour. Even when females are present in a herd, the males often gather together apart from them and neck and mount each other. One male even erected his penis and then walked to a bush and rubbed it back and forth among the branches. While he did this his tail was stuck out straight and then curled tightly over his back.

Sexual play is not confined to the adults. I have seen a young male and a baby male sparring, and after they had stopped, the baby stood behind the young male and mounted him.

Fighting

Fighting between two males occurs in varying intensities, of which two degrees can be described—sparring which can develop into serious fights, and serious fights.

Sparring

Sparring, and its less serious relative necking, are directly connected with sex as mentioned in the preceding section. Sparring takes place between two or three giraffe and even between babies and yearlings. If two males are sparring, they stand side by side facing the same or opposite directions. Suddenly, one male lowers his head and swings it at his opponent's head or body ; the opponent tries to dodge the blow so that it will glance off or miss him entirely. The opponent then retaliates by attempting to hit the other one with his horns. The blows are seldom heavy and between bouts of fighting the animals may stand and rub their necks together. Or they may stand quietly apart for a minute or two staring straight ahead, before continuing to fight. Often neither giraffe will move his feet, and the swinging and movement of their necks is very graceful.

Serious fights

These only occur between two males and are much more exciting to watch. In one such fight witnessed in the Kruger National Park by Mr Grant Wiggell, one of the giraffe was knocked senseless and lay stretched out on the ground for twenty minutes before he struggled to his feet and wandered off. In these fights the bulls seldom stand in one place, and when they do their feet are spread apart to allow for a solid stance. The giraffe stand side by side or with their bodies perpendicular to each other between bouts. The blows are very heavy and can often he heard some distance away. Each animal uses the head to deliver blows to the others body and legs. Sometimes the animals wrap their necks together and push against each other with their

bodies. There is a great deal of advancing and retreating in battle ; one pair was seen to circle about a tree at least ten times, hitting each others flanks. Between bouts the giraffe may rest motionless, or they may walk along side by side for ten yards or so, looking straight ahead, perhaps with their necks stretched out parallel to the ground. Sometimes after blows they put their noses in the air as if stretching or trying to appear taller.

These serious fights may change imperceptibly into sparring matches. I noticed one of a fighting pair trying to neck with the other male and even browsing at a bush between bouts, but he had to keep retreating under the volley of blows from the other who seemed to be much more belligerent.

Fighting among the males is very common, and takes place at any time of the day or year and regardless of the presence of any other male or female giraffe. The hair on the horns of the adult males is always completely worn away by these battles. Even baby giraffe fight and I was interested to see a baby male sparring between two adult bulls. They hit him gently from both sides, and the baby between them waved his head about in all directions, sometimes completely missing both of them.

Even in the fiercest fights, the two males may suddenly stop fighting and both begin eating at the same bush. In two encounters however, the males were not merely exercising, however strenuously, but seemed to be fighting for the leadership of the whole herd. The seriousness was shown by the giraffe completely ignoring the cars and people which were close to them. The first encounter was seen and partly filmed by me in late September. The second encounter occurred in the same place and in the same group and served to confirm events noticed in the earlier battle. This latter battle was witnessed by Mr R. Godet and partly by Mr A. Matthew on the 5th January, and their account is given as the " January battle ".

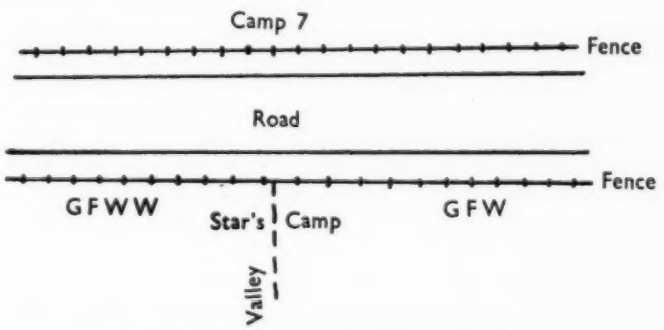

Fig. 6.—Location of the September and January Battles.

In the field marked GFWW there were at least four males, including the very big bull called Star, and across the road in Camp 7 there were four other males in a group. About 7 a.m. while the other giraffe in his field were fighting and eating, Star walked over to the fence and stared across the road at the giraffe in Camp 7. A dark male in this camp stared back at him. They both ignored my car which was parked in the road about thirty yards from

both of them. They stared at each other unwaveringly for a minute, and then Star stalked right up to the fence. The other male then moved closer to his fence. They continued to stare at each other intently for a minute or so, and then the dark male seemed to lose his nerve, for he turned and ran fifty yards back from the road. I am convinced that this was more or less of a psychological battle which Star won without any exchange of blows, rather as though there were an established peck order which the dark male was challenging. Star walked toward the other males in the field, and they all retreated before him, the two fighters breaking off their battle and one of them cantering into the bush. Star occasionally looked back at the dark bull, but the dark bull kept well back in the bushes and was still there the next morning, although some of the other males had jumped over the fence and joined the herd in Star's field.

Three males in Camp 7 then walked up to the fence and Star approached his fence again to stare at them. Star stretched his nose high in the air, one of the three bent his neck down, and the three males turned and moved away from the fence. Then one of them, a light bull, came back and crossed his fence and crossed the road so that only one fence separated him from Star. He and Star then walked about two yards apart, and with the fence between them, for about thirty yards. Then they both stopped and looked straight ahead, Star spreading his legs apart to get a good stance. Suddenly Star whipped his head back and gave the light male a very heavy blow on the chest, the impact of which I could easily hear at eighty yards. The light male staggered back into the road. Just then a car drove up and the light male had to cross the fence into Star's field. The two bulls then edged into the bush, pushing each other and waving their ears and each occasionally giving a surprise blow to the other. Then seven males could be seen in the bush, walking abreast, then in single file and then in circles, making an extraordinary display which remains quite inexplicable. I am sure that Star was superior to the other males in his field, and that both the dark and the light males attempted to challenge his position, with varying success. After this battle Star continued to stay with the herd in his field, and he was the only bull ever seen mating with a female in the herd.

January Battle

In the preliminaries, a blond bull that was not Star was pacing backwards and forwards for 300 yards in each direction beside the fence that divides Camp GFW from the road, and the chocolate coloured male in Camp 7 was pacing opposite him. The blond bull passed an African at a distance of six feet, which shows how preoccupied he was. The blond bull made several motions as if to cross the fence but did not. Then the chocolate bull jumped his fence and crossed the road toward the blond bull. They stood for a minute shaking their ears with their heads close. The chocolate bull took a wide neck swing and gave the blond bull a heavy blow on the ribs from across the fence. The blond bull then returned the blow, at the same time knocking down the fence, and the fight then continued on the road. The animals aimed at each other's ribs, belly or legs and the impacts were such that at times one

would be thrown sideways for several feet and would lose his balance momentarily. The fight lasted for about ten minutes with four or five blows followed by short pauses. The ferocity of the battle was such that Mr Godet expected a fatal ending. Finally the blond bull lost heart and got entangled in the fence while trying to retreat. The chocolate bull administered a volley of blows on his hind quarters before the blond bull could back away from the fence and jump over it a few yards farther along. The blond bull then cantered away into the bush with the chocolate one in dignified pursuit. After this battle, the herd in the blond bull's Camp accepted the chocolate bull without opposition, and although the blond bull tried to rejoin the herd several times, the chocolate bull finally succeeded in driving him away to some distance. The next day, the chocolate bull was still with the herd and seemed quite unafraid of the observer, Mr Matthew, who even wondered if the bull might attack him when he approached.

In the September battle and afterwards, Star remained with the herd and presumably did not lose the fight. If however he was a leader in this herd, it would be expected that he would have taken part in the January battle. It seems therefore that these battles are between individuals and need not concern the leading bull in a herd, if indeed one can be called a leader.

In this herd there was no obvious leader, and it was composed of at least six adult males who were free to sniff at and collect urine from any of the females. The herd was spread out and if there was a leader, as Star may possibly have been, he could not have enforced a privilege such as being the only one that could mount the cows.

A third fight seems to have taken place in June, as both the chocolate bull and Star received neck wounds then. The chocolate bull appeared to have been the victor, as he took over two females that had formerly belonged to Star. Star was left with three babies and the mother of the youngest baby, which was not yet weaned.

Babies

New-born calves have been seen at Fleur de Lys in nearly every month of the year ; breeding is therefore not seasonal. The gestation period is about 14 months and 6 days (Stevenson-Hamilton, 1947). There is usually a single birth although twins are not very uncommon. The calf is about six feet tall at birth and weighs about 120 lb. About one hour after birth it can stand and suckle.

Baby giraffe are more active than the adults, often running for no apparent reason except excess of energy, or lying down and getting up again at five minute intervals. The young and babies in a herd tend to keep together, either lying down beside each other or feeding at the same bush or sparring together. They may wander as much as 100 yards from the herd during the day. One baby was seen with a big male in a herd of seven males but though I watched for an hour no female appeared. Another baby was seen in a group of ten males and no female was in evidence. This evidence of a rather weak maternal instinct is further corroborated in the incident mentioned in the section on jumping fences. In this case the mother left her very young baby

on the other side of the fence, and although she stayed near it she did not cross the fence again and the baby presumably wandered off and died for lack of care.

Babies are often seen in family groups rather than with larger herds. When a person is watching them, the female is usually very nervous and refuses to let the young suckle. In two cases, in family groups, I have seen the babies rounded up by the male and herded off, and in neither case did the mother pay any attention to the babies or even walk behind them.

Communication

The most obvious need for communication occurs when danger threatens, but on such occasions, as well as on any other occasion, I have only once been able to find any sign of communication between giraffe. In this one case, a man approached the big bull Star and a baby that was standing beside him. Star watched the man walk closer and then he snorted and the baby immediately ran off ten yards before stopping to look around as though wondering why he was the only one running. Perhaps such alarm signals are only given by the adults to their young. I have been sitting under a tree while seven giraffe have been browsing toward me, quite unaware of my presence. At forty yards one of the giraffe stopped feeding to stare at me, but the others did not notice me until their attention was directed by his attitude, and it was four or five minutes before all of them knew that I was there. Twice one giraffe of a pair saw me behind a tree, and after staring for a while walked off in the other direction, the second giraffe following without ever looking my way. Another time I walked toward three giraffe, two of which were watching me and the third of which was feeding. I walked to within forty yards before the feeding giraffe casually looked up, startled by several other giraffe in the bush that had stampeded.

Panic seems to be the important factor in spreading the alarm and if one giraffe begins to run, the others stampede after it, sometimes in bush so thick that I doubt if they know what they are running from. Such a case of panic occurred when a female got something in her nose. After rubbing her head and sneezing, she suddenly galloped over to a bush fifty yards away. Two males and a female had been feeding near her and when she rushed off a female galloped after her for about twenty-five yards, one male ran fifteen yards and the other male merely looked around. Some giraffe are more timid than others. Panic may also be more imaginary than real. I walked within 100 yards of a herd that stood nervously watching me and it was not till I had walked away and was 115 yards from them that they stampeded from me.

If more than one giraffe were watching me approach, they invariably moved closer together as I got nearer, until they were forced to retreat.

Interspecific friends

Herbivores are generally gregarious, sometimes with other species. At Fleur de Lys, however, I once watched a female giraffe walk to a tree under which seven wildebeest were lying, and they immediately got up and moved off. Again a young domestic heifer approached a herd of six young male giraffe, and one of the giraffe left the herd to chase her away.

Often when a herd of cattle are advancing across a field while grazing, a giraffe in their way will move to some other part of the field. In 1952 an old male giraffe kept a harem of sixty domestic cows at Fleur de Lys, refusing to let the domestic bulls near them for a month. Two other giraffe joined him for a week and then all three left the cattle in peace.

HERDS

A herd of giraffe is a very loose association, individuals often joining and leaving it. The herds do not show a definite pattern of leadership as is found in many of the ungulates, but there is always at least one big male in every mixed herd and he may be the dominate one.

Leadership

In family herds, the group may be led by the female, but in three cases I have watched it is the male who rounds up the young giraffe and herds them in front of him. Twice I have seen family herds of six walking in single file with a female leading and a male bringing up the rear. However in two other cases I have seen males lead the herd, once by manoeuvring a female away and once by rounding up two young and herding them off. In both cases the rest of the herd followed slowly after the male. In a herd of fifteen giraffe that passed my parked car, a big bull led the way and stood nearest the car to watch it, while the rest of the herd circled round behind him. As the herd was walking away, the bull at the rear watched me until the others were far ahead before he turned and followed them.

The biggest males are superior to the smaller males, and a medium size male will move away from a female if a big bull approaches them. In the September battle already described the four males near Star all moved aside as he approached them.

Individual characters

It was interesting to note individualism among the members of a herd. In one instance three females walked by me at thirty yards. The first in line was fairly bold and chewed and browsed as she walked. The second did not browse but stared at me as she passed, and the third female was very nervous and kept stopping to stare at me and did not browse or chew.

Again one giraffe in a group sometimes watched me for much longer than the others, or kept farther away from me. When drinking at the cattle trough, the most nervous giraffe may not drink at all, while the boldest one may show no hesitation in approaching the water.

Herd composition

As well as the herd in the Game Reserve Area I was able to recognize four groups in other camps. These groups stayed in their camps when there were babies present who could not cross the fences. The number and sexes of the giraffe in the groups studied varied considerably ; either giraffe were frequently

joining and leaving a group, or else the bush was so dense that I was unable to see all the giraffe present. Probably both these possibilities help to account for the varied numbers.

When I toured through Camps 7 to 12 in my car, I made a record of every giraffe or giraffe group that I saw, noting down the number present and their sexes where possible. Data from observations in the Game Reserve Area were not used. There was only a limited number of giraffe in this area (less than twenty) and as I saw them nearly every day, any unusual sex ratio would be far more heavily weighted than results from the other camps which contained more giraffe but which were visited much less frequently. I have records for 141 groups, but of these I was only able to distinguish the sex of all the giraffe present in eighty-one cases. In those cases where the sexes were not ascertained, it seems highly probable that the count also is incomplete ; these records therefore have not been used in any of the work on herd analysis. Where the sexes were ascertained, the giraffe were either in a fairly open area, or near the road, or very patient, so that I could make certain of their sexes. In these cases the count of each herd should therefore be quite accurate.

Of the eighty-one sexings, thirty-two were single animals, twenty-four of these males and eight females. All the other records were for groups and the composition of these are shown in Table 3.

TABLE 3

Composition of giraffe herds

Herd				No. of camps the
Females	Males	Babies	Frequency	combination seen in
0	2		9	6
0	4		3	3
0	5		3	2
2	0		3	3
2	2		3	2
2	3		2	2
0	1	1	2	2
0	3		2	2
0	6		2	2
1	1		2	2
0	4	1	1	1
0	3	1	1	1
3	7		1	1
2	5		1	1
1	5		1	1
0	7		1	1
5	2		1	1
1	3		1	1
		2	1	1
0	3	2	1	1
1	0	1	1	1
0	2	3	1	1
3	3		1	1
3	1		1	1
3	0		1	1
1	4		1	1
2	1		1	1

From these results, it is evident that a single male is nearly three times as common as any other arrangement of one or more giraffes and that two males together rank as the next most common, closely followed by single females. Of the larger groups, male companies of up to seven bulls were relatively common, while females were seldom seen without males, and mixed groups with over three females were never seen.

The total number of females was forty, and of males 101. I do not know why so many more males were seen, but it would be most unexpected if such a difference actually existed. It is interesting to note that babies were most frequently seen in groups of males when no females were present.

To study the groups more closely, the sizes of the giraffe were noted as well as the sex. For more extensive results, records of giraffe from the Game Reserve Area were included in this study. In this area the groups were large and the number of solitary males and females of the various sizes should help to clarify the group structures.

The sizes of the giraffe were judged very approximately but as closely to the scale below as possible.

	Males	Females
Big	over 15 feet	over 13 feet
Medium	11′–15′	10′–13′
Small	8′–11′	8′–10′
Baby	under 8′	under 8′

Of all the single bulls that were recorded for size, eighteen were big and three were medium. Of the females, four were big and two medium.

Where two bulls were seen together, their sizes and the frequency with which they were seen were noted.

	Frequently seen
Both bulls big	6
Both medium	1
1 big and 1 medium	4
1 medium and 1 small	2
1 big and 1 small	1

These figures show that big bulls are more often seen away from the larger groups, but that bull pairs may even include small animals.

Bull herds

A table of the number and size-composition of bull herds is given in Table 4 for numbers of bulls greater than two seen together.

These bull herds are a distinctive feature of giraffe social life. There appear to be three types. The most common type, as in herds 1 to 8, consist entirely or predominantly of large bulls. In the second type, herds 9 and 10, the groups impressed me as resembling a school with a big bull in charge of the younger giraffe. In the group of six, the five younger ones followed each other in single file and kept near the big bull which was the only one browsing. Finally he rounded them all up ahead of him and herded them off into the

TABLE 4

Composition of bull herds

No. of herd	Babies	Bulls			Frequency seen
		Small	Medium	Large	
1				7	1
2				3	1
3			1	3	2
4		1	1	3	1
5			2	2	2
6			1	2	2
7		2	1	2	1
8		1	1	1	1
9		4		1	1
10		5		1	1
11			3		1
12		1	3		1
13		1	4		1
14		1	5		1
15		1	6		1
16	1		2	1	
17	1		1		
18		1		1	

bush. The third type, herds 11 to 15, are probably those males who are too old to stay with their mothers, but who are not accepted into the mixed herds as adults. Herds 16 to 18 will belong to the first type although in these cases the medium or big bulls have a baby or young giraffe with them. These bull herds spend most of their time browsing, fighting, and occasionally mounting each other.

TABLE 5

Composition of groups without males

Cows			Babies	Frequency seen
Small	Medium	Large		
		2	3	1
		3	2	1
	1	2	2	1
1	1		2	1
		1	1	1
		3		1
		2		1
2		2		2
	2	1		1
	1	1		1

Nearly half the female groups listed in Table 5 contained one or more babies, and often very young babies which may have been born less than a week earlier. The rest of the herds all had at least one big female. These groups are much less distinct than the types of bull herds already noted. In several cases, medium sized females had babies so that both big and medium females come under the adult class.

Mixed herds

The composition of mixed herds is detailed in Table 6 from which it will be clear that mixed groups are very varied. The majority have only one big male, but others have up to eight males, a fact which precludes the possibility of groups being compared with harems having only one big bull and possibly other young bulls, as in many species of ungulates. Among both males and females the small animals number about one-eighth of the two larger groups of animals of the same sex. The babies only form 6 per cent of the total number.

TABLE 6

Composition of mixed herds

Total	Cows			Babies	Bulls			
	Small	Medium	Large		Small	Medium	Large	
9		1					8	
15		4	1			4	6	
15	1	3	2			3	6	
9		2			1	1	5	
7		2				1	4	
6			1			1	3	
7		2				2	3	
6	2	1	1				2	
6		1				3	2	
8		2		3		1	2	Twice
6			1	1	1	2	1	
10			7			2	1	
6	1		2			2	1	
8	2	1	1	1		2	1	
5		1		1	1	1	1	
6	1		2			2	1	
5	1		2		1		1	
5		1	1		2		1	
11		2	1	1	3	3	1	
5		1			1	2	1	
3		1				1	1	Thrice
4			3				1	
6			2	1		2	1	
3			1	1			1	Twice
4		1				2	1	
4		2				1	1	Twice
4		2	1				1	
3			2				1	
2	1						1	
2		1					1	
4		3				1		
6		2	2	1		1		
5	1			3	1			
6		1	3			2		
5			2		2	1		
	—	—	—	—	—	—	—	
	10	37	38	13	13	43	61	

TABLE 7

Composition of herd in Guernsey and Game Reserve Area

Place	Time	Date	Individuals								Types							Comments
			Star	Pom-pom	Twins	Pim*	Cream	Limpy	Starlet*	Rotic*	Big Males	Big Females	Med. Males	Med. Females	Young	Babies	Total Herd	
GFWW	8.00	Sept. 29	–								7			1			8	Day of Sept. Battle.
GFMRd	12.00	,,									8			1			9	,, Male following female.
GF	11.00	Oct. 8									1	3	1	2	3	1	11	
GFVS	7.00	,, 15	–	–	1						5	1	4	2			15	Star edged ♂ away from twin.
GFSS	3.40	,,	–		1							1					8	
GFSS	10.30	,, 16															Herd	
GFSSW	9.30	,, 17														1	13	
GFSSW	9.00	,, 18															14	
GFMRd	4.15	,,	–	–								1	2	2		1	8	
GRCrVS	11.30	,, 20	–	–	1						4		1	1	m	1	10	
GRLCiVS	8.00	,, 22															6	
GRLCiVN	8.15	,,	–										1	1			3	
GRLCr	10.35	,,	–	–							1	1		2	m		7	Star following Pom-Pom.
GRLCiVS	5.00	,,	–	–									1				3	Star mounting Pom-Pom and other male watching.
GRUCiVS	7.15	,, 23									2		2				4	
GRAF	8.55	,,									5		3				11	
GRCr	4.40	,,									2		1				3	
GFSS	6.15	,, 24	•														10	
GF etc.	9.00	,,															18+	Limpy and other strangers with herd.
GFSSW	5.00	,,	–	–	2												15	Limpy followed me. Star sniffed his tail.
GF	6.45	,, 26	–	–	2								1			3	11	Star sniffed at Pom-Pom and other male withdrew.
GF	9.40	,, 27					–						3	1				Cream often alone. Two males withdrew before him.
GRCi Loop	11.20	,,	–	–	2						3		1		m	m	10	
GR Join VS	9.15	,, 29	–	–	2		–									1	9	
GRLCiN	4.15	,,	–								1		2				4	
GRAF	5.00	,,	–	–			–				1	2	1	1	m	1	11	Cream in middle of herd and Star farther off.
GRLCiVN	7.05	,, 15	•								2		1	2	f	1	12	Star and two males feeding farther off.
GRAF	8.00	,,	–	–												3	7	
GFVW	4.30	,,	–								2		1	2			9	Walking in single file with Star ahead.
GRAF	4.00	,, 16	–						–				1		m	1	9	
GRCr	9.00	,, 17			2												10	

GRCi Loop	11.20	,,	–	–	2					3		1		m	m	1	10	
GR Join VS	9.15	,, 29	–	–	2		–									1	9	
GRLCiN	4.15	,,	–				–			1		2				1	4	
GRAF	5.00	,,	–	–			–			1	2	1	1	m		1	11	Cream in middle of herd and Star farther off.
GRLCiVN	7.05	,, 15	–	–						1		2	2	f		1	13	Star and two males feeding farther off.
GRAF	8.00	,,	–	–												2	2	
GFVW	4.30	,,	–	–						2		1	2			3	7	
GRAF	4.00	,, 16	–					–				1		m		1	9	Walking in single file with Star ahead.
GRCr	9.00	,, 17	–		2					6				m		2	9	
GFW	1.30	,, 18	–	–						4			1				10	
GFVE & GF	12.00	,, 19	–	–	2					5							7	
GFS	9.00	,, 21	–	–													9	Five in single file with Star at rear.
GF & GFVE	6.30	,, 22	–	–	2					6				1		2	9	
GFW & GFS	9.45	,, 23	–		2					3		1		m			15	Six males off apart in GF.
																	14	Six in single file, twins, two young and then two males.
GRCiJoinN	12.00	,, 24		–	2	–				3		2				3	12	
GRAFW	7.25	,, 25						–		2							3	
GFS	7.30	,, 26	–	–	1					2			1				6	Star alone in GFSS as if meeting the rest.
GF & GFW	2.00	,, 27	–							6							7	
GFVE & GFS	6.45	Dec. 3	–	–	1					3							6	Star following twin.
GF	6.45	,, 4			1					1		3					5	
GFVE	6.40	,, 5	–	–	1					3							7	
GFVE	2.15	,, 6			1												2	
GFEF	11.30	,, 7		–	1					1							4	
GFVE	2.55	,,	–	–	1					1							6	
GFWW	7.30	,, 8	–														7	
GRUCi	9.00	,, 10	–	–	1	–	–			2	1		2	m	m		12	
GRAFE	8.50	,, 11								2	1	1					4	
GFSS	10.15	,,	–	–					–		1		2		1		11+	
GFSS	1.15	,, 13	–	–	1										1		Herd	
GFVS	8.00	Dec. 18		–				–	–	3		2	4	m			13	
GFAFE	6 p.m.	,, 25		–	2				–			1		1			6	
GFW	10.00	,, 27		–	1				–	4		1		m	1		15	
GFVE	5.15	,,			1							1					2	
GFSSE	11.00	,, 28															6	

* indicates that the giraffe was not individually recognized until towards the end of the observations ; m=male ; f=female ; 6–12 o'clock =morning ; 12—6=afternoon unless otherwise stated.
Twins=two medium-sized females which were distinctly reticulated but which could not be told apart.
Star=a big male with star-shaped markings.
Pom-Pom=medium-sized female with prominent tufts of hair on her horns.
*Pim=a light coloured medium-sized female.
Cream=a big male with dark spots and a pouch of skin between his forelegs.
Limpy=an emaciated big bull with a lame front foreleg.
*Starlet=a big bull with star-like markings.
*Retic=a big bull with thin white reticulations between his spots.

I was interested in the behaviour of a bull herd at Fleur de Lys. Star walked slowly by himself over 400 yards, stopping at intervals to look round or nibble at a bush. When he approached the dense bush near the river's edge, he stood there for about ten minutes looking around. Then five giraffe came out of the bush one by one ; I think that they had just crossed the river. Star joined the other giraffe and they all moved off away from the river. I had the impression, perhaps anthropomorphically, that Star had known that the giraffe were coming and had gone to wait for them. Star came from over the hill so I doubt if he could have seen them before getting fairly close to the river.

Game Reserve herd

The herd of fifteen or so giraffe in the Game Reserve Area were studied, particularly from October to December and in April and May. This herd contained a number of individuals that were recognizable on sight so that in these cases the individual's relation to the herd became clearer. Table 7 included here gives the records for time, place and giraffe seen in the Game Reserve Area during the three month period.

The places referred to are marked on Fig. 5. The area is divided into two parts on each side of the river, the Game Reserve and the Guernsey Field.

GF —Guernsey Field and central area.
GFW —field west of the Guernsey Field.
GFWW —field west of GFW.
so also GFS, GFSS, GFSSW, GFSSE, GFE, etc. (E–east, S–south, W–west).
GFMRd—GF area by the main road.
GFCr —GF area near the Cross Rd.
GFVE —Valley to the E of the GF.

The Game Reserve can be divided into the UGR and the LGR, meaning the upper and lower parts of the area.

GRAF —Agave Field.
GRCr —Game Reserve area near the Cross Rd.
LCi —Lower Circit Road.
UCi —Upper Circuit Road.
UCiVS —Valley south of UCi.
CiLoop —Inside the loop of the Circuit Rd.
CiJoin —at base or west end of circuit loop.

The most remarkable fact about Table 7 is that it reveals how loose the association of giraffe in a herd really is. This may be due to the lack of predation experienced at Fleur de Lys. From day to day and even during one day, different giraffe are found grouped together in varying numbers, so that the individuals are continually leaving one group and joining another. This tolerance is indicated by the individuals Limpy and Cream. Limpy belonged to a non-Fleur de Lys emaciated herd, and Cream was usually seen by himself. Yet both these big bulls were found several times and for short periods right

in the middle of the herd under observation, and none of the members of the herd took exception to their presence.

Star is an example of the individualism found in giraffe. He was often present with other males and females but he was sometimes alone or with a group of males. These herds might be large or small. He sometimes led the herd and sometimes brought up the rear but often he paid little or no attention to the other giraffe at all. He sniffed at and collected urine from other females as did the other males. However he was the only male ever seen mating or trying to mate. His partner in the successful mating was Pom-Pom and she was more often in the same group as Star than either of the twins or the other females.

Between mid-April and mid-May I was able to study a family herd closely. The nucleus of this herd consisted of Star, three or four females and three babies, belonging to three of the females. Star was interested primarily in the mother of the biggest baby, rather than in the other members of the group. He would follow this female about for days on end, always standing behind her or feeding beside her and occasionally collecting her urine. He ignored the rest of the herd, other than once to snort an alarm at one of the babies when a man approached. This female would occasionally let her baby suckle, but once Star chased the baby away by snorting at it, when it came between its mother and Star who was following the mother. Sometimes Star's group would include only two females and two babies, and once the third female and baby were seen away from the herd with another big bull. In another instance a female and the three babies were alone and a big male approached them and collected the female's urine and then they all browsed together. Occasionally Star's group joined another mixed group of giraffe, and Star took no notice if a male collected urine from any of his females, or if they touched any of the babies. Star was even seen completely away from the herd and browsing with two big bulls. He was not always so indifferent and once he found one of the females walking and feeding with a big male. He immediately rushed at the male and chased him away. Then he stood between the male and his group of four females and the three babies, so that the male could not approach them again.

On June 1st the cows and the three babies were seen being squired by the chocolate bull of the January battle described above. Both he and Star had fresh wounds on their necks and presumably there had been a serious fight between them. On the following day Star was seen with the mother of the youngest baby as well as the other two babies. The chocolate bull had gone away with the other two females.

From these observations, it seems that it is the females who are on heat or coming on heat, that attract the males, and that the males do not act as leaders and are not even particularly interested in the other females and babies in a group. The females are often reluctant to suckle the babies, and as the babies are able to browse at a very early age it is possible that the babies are weaned perhaps forcibly when they are quite young. The females may then come on heat again, which would explain the male's interest in them at this time.

The chocolate bull who seemed to have beaten Star and taken over his herd, was thus only interested in the two females whose babies were fairly large and who were likely to be coming on heat. Their babies were forcibly weaned and left with the mother of the youngest baby and with Star.

MOVEMENT

The giraffe in a herd do not move about and feed at random, but all head in a particular direction, each giraffe apparently independent of the others and walking and feeding at his own tempo. There is no clannishness in their behaviour, as there is in herds of sable, kudu, waterbuck and wildebeest.

To find out how far and how fast a giraffe troop moves from day to day, the positions of the herd of fifteen in the Guernsey Field and Game Reserve Areas were noted whenever possible from the middle of October to the end of December. Observations were always made from a car and at some distance from a herd so that the giraffe would not be disturbed. The records are shown in Tables 8 and 9.

TABLE 8

Daily movements

Date	Time hours	Speed yds./hr.
Oct. 15	4	264
15	4·5	126
16	0·5	162
18	7	127
24	11	65
26	4	51
29	8	172
Nov. 13	4·5	108
14	6·5	72
15	8·5	222
17	3	392
19	3·5	87
21	3·5	145
22	2	142
23	1·5	459
24	2	446
26	4	142
27	2·5	332
Dec. 3	1·5	432
4	0·5	324
5	1·5	203
7	1	0
7	3	68
10	1	243
11	3	338
27	1·5	837
Means	3·6	229

TABLE 9

Minimum nocturnal movements

Date	Time hours	Speed yds./hr.	Distance yds (over 20 hr. period)	
Oct. 15	19	11	220	
17	22·5	38	760	
18	24·5	0	0	
23	20·5	39	780	
24	23	36	720	
27	24·5	113	2260	
30	13	117	2340	
Nov. 14	20·5	144	2880	
15	15·5	84	1680	
16	23·5	80	1600	
17	17	20	400	
			——	Aver.
18	26	125	2500	1240
19	22	40	800	
22	18	38	760	
23	26	28	460	
24	24	96	1920	
27	26	47	940	
Dec. 4	22·5	36	720	
5	23·5	14	280	
8	16·5	90	1800	
11	25	78	1560	
28	24	37	740	
Mean	21·7	60	1200	

Table 8 deals with herd movements during the daytime, observations lasting from half-an-hour to eight and-a-half hours, and the rate of movement

is given in yards per hour. These observations were made in the morning or afternoon, and no account is taken of what the giraffe were doing at the time, as the collection of such particulars make the census too difficult when some members of the herd may be walking or browsing while others are lying down or chewing.

Table 9 deals with the movement of the herd overnight. The position of the herd was noted in the afternoon and again the next day, from thirteen to twenty-six hours later, depending on when the herd could be located. The rate of travel in this case is the minimum and based on the straight line distance covered although the herd may have taken a longer and more circuitous route. Taking a rough average of the time during which the movement was calculated as twenty hours, an estimate of the distance covered each night was obtained.

The movement in Tables 8 and 9 does not seem to be correlated with the time of year, even though it may have been expected that greater distances would be covered during the early part of the year when food was relatively hard to find. No correlation was found either with rainfall, sunshine, temperature or humidity when these were plotted on graphs, so that the weather seems to have no influence on the movement of the giraffe.

In conclusion it can be stated that a herd of about fifteen giraffe can live in an area of 2000 acres for at least eight months without leaving it. Such a herd travelled a mean distance of 1200 yards, or less than a mile a day in a twenty hour period including night-time. During the daytime it averaged a rate of 229 yards, or less than one-seventh of a mile, per hour. When one considers that a giraffe can maintain a speed of thirty m.p.h. when running, this daily pace seems very slow indeed.

Two cases of troop migration were observed. In the first, the day after a large area east of the main road was burnt out, a herd of eleven giraffe were seen several miles west of the road, where they had seldom if ever been seen before, presumably driven out by the fire. In the second, during the dry season, a strange herd of thirteen emaciated giraffe was found in the Guernsey Field. About thirty miles north of Fleur de Lys the country was extremely dry and all the giraffe there were equally thin. It seems likely that this herd had migrated from the north to the Klaserie Valley where food was more abundant.

SENSES

Sight. The sight of the giraffe is excellent, and I have often noticed a giraffe watching me from a distance of a quarter of a mile.

Hearing. Any sound that I heard was always heard by any giraffe near me. The approach of cattle, cars or Africans, the cough of a sable antelope, or a distant train whistle, always caused the giraffe to stop and turn to face the direction of the sound.

Smell. There is some controversy regarding the acuteness of the giraffe's sense of smell. On two occasions I have watched giraffe facing me and bending their necks down as if testing the air, but without experiment it is impossible to judge how efficient the sense of smell may be.

PHYSICAL FEATURES

Colour. Among the giraffe at Fleur de Lys, the colour tends to darken with age, particularly among the males. The protective colouring is most impressive and in the bush even at fifty yards I have detected one giraffe with difficulty while overlooking seven or more near it. Although giraffe are so well camouflaged, they often stick their heads out inquisitively from behind a bush so that they are instantly observed when they might otherwise have escaped notice. They also betray their presence by whisking their tails about to drive away flies, and by a similar action when they are alarmed.

Health. The giraffe on Fleur de Lys always looked in remarkably good condition, even during the later part of the dry winter. One bull, however, had ugly growths sticking out on the lower part of his neck. There were two cases of lameness, one caused by a snare. Several young giraffe had large grey or black areas of scab on their necks and upper backs around which flies collected. One medium sized bull had a flop ear, probably due to a tick infection.

Noise. Giraffe are not silent, as was formerly believed. I have often heard them snort, always when looking at me. If I sat on the ground and stayed perfectly still the giraffe would snort at short intervals while watching me, in the same manner as suspicious kudu and other antelope. Other sounds I have heard giraffe make include a " hunh ", a sneeze, and a frequent loud breathing or blowing, all these sounds being emitted while the animal was looking at me. I have never found evidence that they use noises to communicate with each other.

MISCELLANEOUS ITEMS

Fire. When there was a veld fire near Fleur de Lys, the giraffe panicked and rushed about, sometimes right into the fire. The cattleman tried to steer one group of three away from flames closing in on three sides of them but they refused to move. In this grass fire, the browse of the giraffe was largely untouched and they could easily have stepped over the flames.

Night. In the dry season, four giraffe were seen eating at 9.30 p.m., several hours after sunset. Later in the season, on a tour at 8.30 when it was dark, one giraffe was found drinking, a baby and a cow were lying down while a bull stood nearby, and at least four others were found standing in the bush.

Shade. Although I have often noted the number of giraffe in a herd lying or standing in shade or in sunlight, I have been unable to note any preference for either position. Giraffe can often be seen standing around one or several trees, but they also stand or lie in open fields away from the shade. The great thickness of the hide of the giraffe may be the reason for the animals' apparent indifference to exposure to direct sunlight.

Birds and Ticks. Tick birds, *Buphagoides erythrorhynchus*, are often seen around the giraffe at Fleur de Lys. They peck round the heads of the giraffe, slide down their necks and even run about upside down on their stomachs. If danger is near, they fly up and give the alarm to the giraffe.

Three species of tick were present in large numbers on a large bull that was shot at Fleur de Lys. Doubtless other species also attack the giraffe. The species found were *Amblyomma hebraeum* the bont tick, *Boophilus decoloratus* the blue tick, and *Rhipicephalus appendiculatus* the brown tick. These ticks are vectors respectively of heartwater, redwater and East Coast fever in cattle but the susceptibility of other game and the giraffe to these diseases is at present unknown.

Distances. Hediger (1950) made a study of escape reactions, recording the minimum distance at which various animals will allow man to approach before they retreat. Out of fourteen observations, I approached giraffe on foot to a mean distance of fifty-one yards, with a maximum escape distance of 100 yards and a minimum of twenty-five yards. Out of twenty-two observations I drove a motor car within a mean distance of thirty-eight yards from the giraffe, with a maximum distance of eighty yards and a minimum distance of fifteen yards.

The individual distance is defined as the minimum distance within which individuals of a species will approach each other, excluding mating behaviour and fighting. For giraffe this distance may be nearly zero when they are feeding, and it is also variable when they are standing and chewing, and about twenty yards when they are lying.

The social distance is the maximum distance between individuals of a species in a group. In such loose groups as giraffe often form, this may be very large indeed, and a very rough estimate might be set at 500 yards.

Photography. Giraffe were never upset by being photographed or even by the noise of a ciné camera. Once however I was parked fifteen yards from a male giraffe who was standing by a fence and watching the car. When I slowly put the unipod out of the window in preparation for taking pictures, the giraffe became terrified and immediately turned, jumped over the fence, and ran off. The glint of metal in the sun or the snake-like shape of the unipod may have been responsible for his panic.

SUMMARY

The giraffe in South Africa live entirely in the Eastern Transvaal, a lowveld region primarily of grass or veld with scattered bushes and low trees. The giraffe browse on a wide variety of trees in the spring and fall when few leaves are available, but in summer when all the trees are in foliage they are much more selective. The giraffe spend most of the day and part of the night feeding, especially the early morning and late afternoon. In the summer when food is abundant, the giraffe have more time during the day to chew their cud and lie down.

The males spend part of the day fighting with each other. Such matches are seldom serious and often end in sexual play with one male mounting the other. The most common heterosexual activity was the testing of the females' urine by the male. There is no breeding season among giraffe, and the young are born all through the year.

Giraffe are usually found in groups or herds, but they do not appear to communicate with each other, although they are capable of making sounds.

The herds are loose associations of animals, generally with no definite leadership, and often include both adult males and females. Herds travelled very slowly, and often remained on the farm where they were studied for at least one year.

The giraffe on Fleur de Lys farm have become used to farm conditions ; they jump fences instead of breaking through them, and drink water from the cattle troughs, often walking among the cattle to do so.

ACKNOWLEDGMENTS

I wish to express my deepest gratitude to Mr Alexander Matthew of Fleur de Lys farm, without whose most generous hospitality this study could never have been undertaken. I am also indebted to the kindness of Dr and Mrs D. W. Ewer of Rhodes University. My thanks are also extended to the following for assistance given by interviews or correspondence, Dr H. Hediger, Director, Zoological Gardens, Zurich ; M · O. Jones, Curator of Mammals, London Zoological Gardens ; Dr L. H. Matthews, Scientific Director, London Zoological Gardens ; Mr G. Robinson, Head Keeper in the Giraffe House, London Zoological Gardens ; Mr Stein and Mr Ketterly, Transvaal Department of Conservation ; Mr R. Douglass, Tanganyika Safaris, Arusha, Tanganyika ; Mr K. Thomas, Department of Game, Tanganyika.

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Ficus petersii

Strychnos spinosa

Acacia woodii

Combretum imberbe

Four favourite food-plants of the giraffe, from which the foliage has been browsed nearly completely to a height of sixteen feet

THE ABDOMINAL MUSCULATURE OF NYMPHAL *CHLOEON DIPTERUM* L. (INSECTA : EPHEMEROPTERA) IN RELATION TO GILL MOVEMENT AND SWIMMING

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(With 7 figures in the text)

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INTRODUCTION

Chloeon dipterum L. as a nymph, inhabits stagnant waters and is probably in many regions the commonest ephemeropteron of ponds. It may be found in all parts of the water body—on the substratum at some depth as well as among water weeds near the surface. It moves with rapidity, propelling itself by means of lateral rhythmical movements of its abdomen which behaves in this respect much as does the tail of a fish in swimming and this in spite of the fact that the fringed caudal filaments lie in the horizontal plane and appear to be more likely to bring about progression in the manner of a whale.

It is thus a pelagic creature and presents a different type of environmental adaptation from those previously dealt with by me, viz. *Leptophlebia*, *Ephemera*, *Caenis* and *Ecdyonurus* (Eastham, 1932 ; 1934 ; 1936 ; 1937 and 1938).

The purpose of this paper is to describe the gills, the currents set up by them over the body and the muscular mechanisms which make these and swimming possible.

The techniques employed are similar to those previously employed except that cinemaphotography has been resorted to to amplify observations made by means of the stroboscope.

The features described here are specific to *Chloeon dipterum* L.

THE GILLS

Figs. 1 and 2.

On each of the first seven segments of the abdomen is a pair of gills borne on the posterior-lateral angles of the segments. Those of the first segment

consist each of a circular plate articulated to the body by a short stalk and carrying on its anterior face a lanceolate lamella. This lies over the middle part of the circular lamella with which it makes slight contact at its distal extremity. The gills of the seventh segment are similar in form to this except that they possess no anterior lamella.

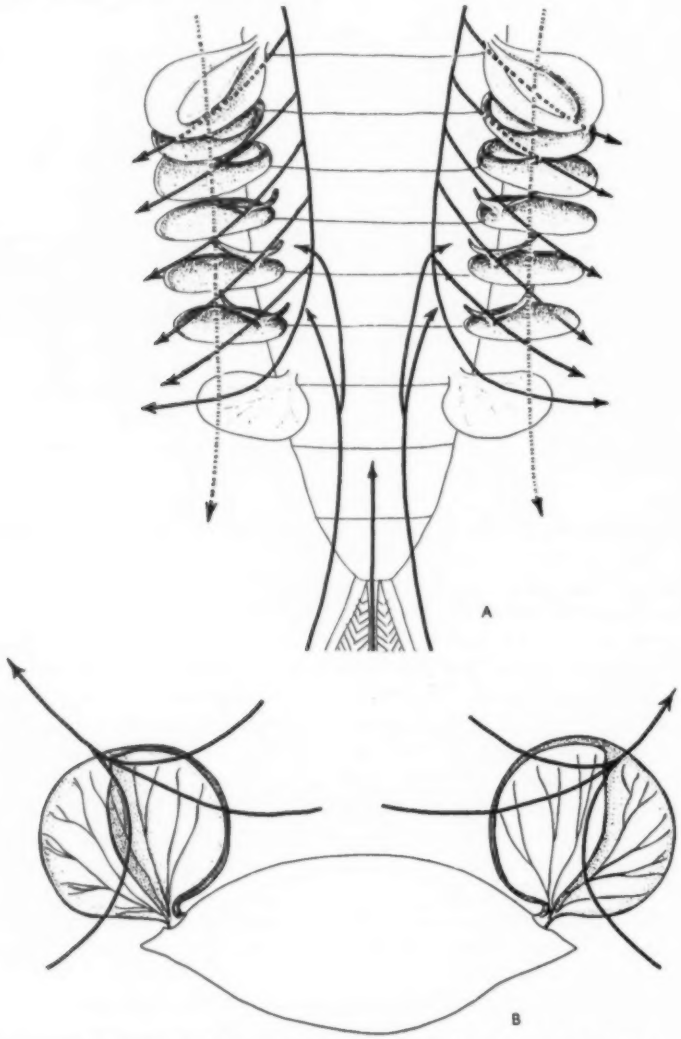

Fig. 1.—A. Dorsal view of the abdomen of *Chlocon* to show the main water currents.
B. Transverse sectional view of a gill bearing segment as seen from in front.

Each gill on segments 2 to 6 is circular in form and concave anteriorly. Its anterior lamella is semicircular coinciding with the median half of the

posterior circular lamella over which it lies (Fig. 1). Each such anterior lamella is also concave in front with its median border turned forwards for all its length and its lower lateral border also turned forwards so as nearly to meet the posterior surface of the gill next in front. For the remainder of its length the lateral edge of the anterior lamella is flat. In motion it will later be shown that the anterior lamella of a gill applies itself to the surface of the gill in front of it thus enclosing a space between them which is open to the environment dorso-laterally where this flattened border occurs.

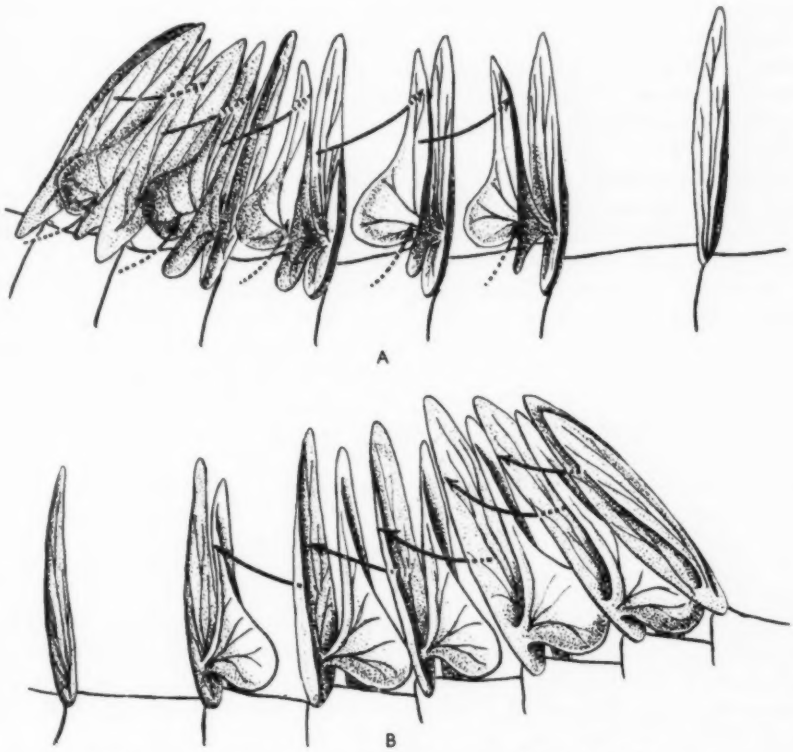

Fig. 2.—A. The gills of the right side as seen from the middle line of the body.
B. The gills of the right side as seen from the outer side of body. Note the gaps between posterior and anterior lamellae of adjacent gills through which water escapes to the side.

The gills are disposed in such a way that their surfaces, held more or less erect, are roughly at right angles to the longitudinal axis of the body. Those of the last gill bearing segment are perpendicular, those in front of it tilting backwards towards them. The more anterior the gill the more is the gill tilted backwards at an angle with the perpendicular, (Fig. 2), thus producing a crowding effect of the anterior gills of a side.

This disposition of gills bringing them into close contact with each other in each lateral series is important in bringing about precise water currents when the gills are put in motion.

THE CURRENTS SET UP BY THE GILLS

Figs. 1 and 2

Only the first six pairs of gills move—the seventh pair remaining stationary at all times, held vertically and turned slightly outwards (Figs. 1 and 2). Movement occurs in short bursts followed by longer periods of absolute rigidity.

Between the two longitudinal rows of gills water passes slowly backwards entering the valley between the gills from in front at each side of the wing cases. This is the median antero-posterior current and from it water is drawn to each side between the gills in a postero-lateral and upwards direction (Figs. 1 and 2).

Water also passes into these postero-lateral currents from above the level of the gills (Fig. 1). Such parts of these currents as pass laterally between the more posterior gills is deflected well to the side by the immobile posterior gill which thus act as buffers giving a pronounced lateral direction to the water.

Movement of water in these ways sets up several induced currents. For instance from above the upcurved cerci and caudal filaments there passes forwards a current reaching as far as the last three gill-bearing segments there to be deflected sideways into the already described postero-lateral currents. Another induced low lateral current passes back at each side at the level of the gill articulations (Fig. 1). This dissipates itself at about the level of the last segment of the abdomen but during its passage it feeds from the sides of the body the postero-lateral currents passing between the gills.

THE GILL MOVEMENTS

Fig. 3.

The gills move in metachronal rhythms from before backwards, members of pairs beating synchronously. This rhythm being of such an order that the second gill is found to be in the same phase of movement as is the sixth. It follows from this that phases of suction and of compression between neighbouring gills in series follow one another with regularity.

When, for instance (i) a gill is in its backward path it is a little ahead of the gill next behind it so tending to close the space between them. On the other hand (ii) when the hinder of these two gills has reached the limit of its backward movement the one in front of it has started to return to its forward position and thus the space between the gills is enlarged. In this example the first is a compression phase during which water is squeezed out from the inter-gill space, the second a suction phase in which water is drawn in to fill that same inter-gill space. The direction from which the water is drawn (suction) and in which it is subsequently forced (compression) depends on the precise form of the gill and the turning movements performed during its oscillations.

The effective space between serially adjacent gills appears to be that between an anterior lamella of a gill and the posterior lamella of the gill next in front of it. This is disclosed by both the stroboscope and by cinematograph films. The spaces between anterior and posterior lamella of gills themselves is fairly constant and little affected by the metachronal movements. It would appear then that the anterior lamella is a device to bridge the gap between neighbouring gills of a series ; this gap being determined by the length of the body segments (Fig. 2).

Let us consider the gills of one side of segments 4 and 5. As gill 4 begins to move backwards, its posterior lamella approaches the anterior lamella of gill 5 which now also starts to move backwards. The lagging anterior lamella of gill 5 is now closely pressed against by the posterior lamella of gill 4 so enclosing a space from which water is squeezed out laterally and upwards at those very points where the lateral border of the anterior lamella is flat and not forward-curved (Fig. 2).

Posterior and anterior lamellae of adjacent gills in series therefore fit together to form something like pipette bulbs with asymmetrical outlets to the sides and upwards.

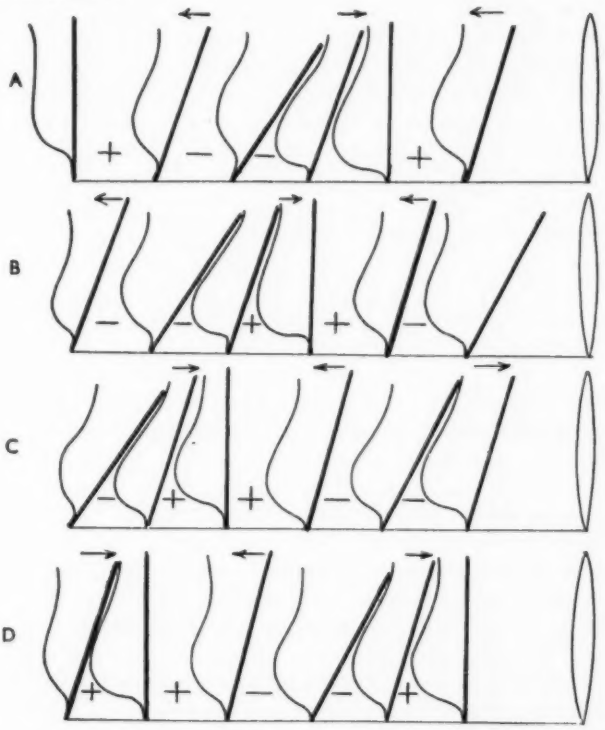

Fig. 3.—A, B, C, D. Four phases of gill movements of a series of one side to show the nature of the metachronal rhythm and the pressures set up between the gills when in motion. For further explanation see text.

A lateral impetus is thus given to the water between these lamella. When next the gills begin to separate from each other as for instance when gill 4 begins its forward movement, water is drawn in from above the middle line of the body. This is made possible by the greater forward curvature of the lateral border of the anterior lamella which tends to maintain contact with the posterior lamella in front of it for a longer time than does its median (less curved) border.

Fig. 2, A and B is an attempt to depict the gills of a series as seen from both median (A) and lateral (B) aspects and there is shown the close packing of the gills brought about partly by the leaning of the gills towards those next behind in the series and the effective filling up of the space between the gills by the strongly curved anterior lamella.

The movements of individual gills—all but one having been removed—were observed and these were seen to be of such an order as to direct water from above the middle line of the body to the side. Each gill in its backward movement rotates on its stalk of attachment so as to turn the anterior face upwards and outwards to the side of the body. In this action not only is water behind the gill pressed backwards but such water as lay on the anterior surface at the beginning of the beat is baled sideways. Such an action clearly reinforces the currents set up by the metachronal movements of the gills in series, but is regarded as playing a relatively insignificant part in current creation.

Fig. 3 is a diagram taken from cinematograph films of the gills in movement and shows in series four phases of gill activity, the rhythm being such that a gill is in the same phase of movement as is the one five segments next behind it. In each of the four phases the stationary erect posterior gill is to the right of the diagram. The direction of movement of the gills is shown by arrows and the pressures set up between neighbouring gills, by + and − signs.

THE ABDOMINAL AND GILL MUSCULATURE

The muscles of the abdomen in gill bearing segments are modifications of the normal longitudinal and dorso-ventral muscles which occur in insects in general.

They serve two functions, viz. to move the abdomen in such a way as to propel the animal through the water and to oscillate the gills so as to create water currents over the body.

Longitudinal muscles Figs. 4, 5 and 6.

On each side of the middle line both ventrally and dorsally strong longitudinal muscles pass between the anterior borders of tergites of successive segments and similarly between the anterior borders of sternites.

Each such longitudinal muscle, whether dorsal or ventral, has a disposition which is peculiar to these animals. Thus taking those of one side dorsally as an example, we find that the main muscle mass of a segment is divided into two bands which cross each other in each segment to produce a cruciform effect (Fig. 4). This is effected in such a way that half the muscle passes from a more median origin on the tergite's anterior border to a more lateral insertion on the anterior border of the tergite next behind it. The other half passes

under this in precisely the opposite direction, namely from a more lateral origin on the tergite's anterior border to a more median insertion on the anterior border of the tergite next behind.

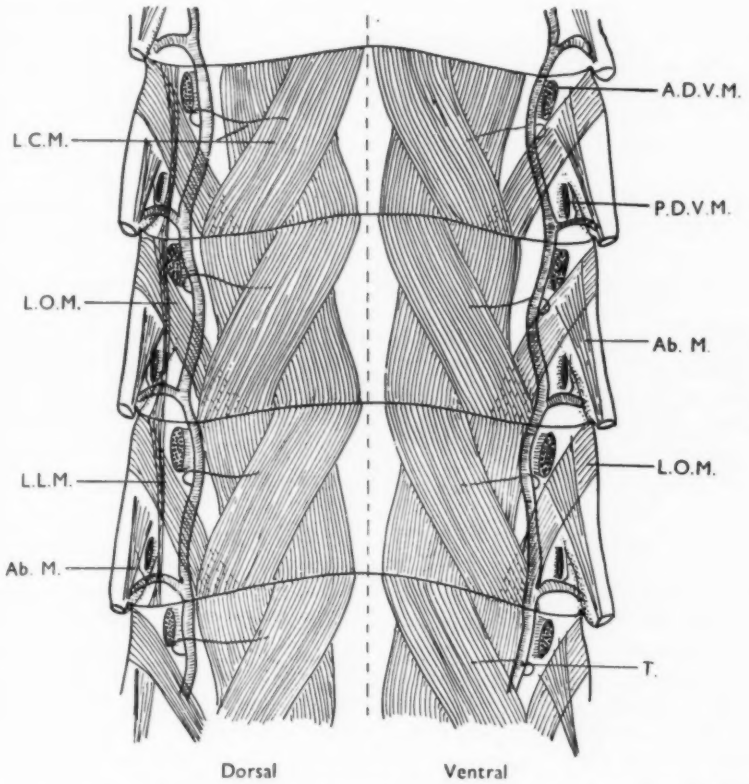

Fig. 4.—The muscles of three adjacent gill bearing segments as seen by transparency dorsally on the left and ventrally on the right.
Ab.M. Abductor muscle ; A.D.V.M. Anterior dorso-ventral muscle ; L.L.M. Lateral longitudinal muscle ; L.C.M. Longitudinal cruciform muscle ; L.O.M. Lateral oblique longitudinal muscle ; P.D.V.M. Posterior dorso-ventral muscle ; T. Trachea.

The plaited appearance which the muscles present is well illustrated in Figs. 4 and 5. A further part of this same longitudinal muscle mass has its anterior origin on the pleuro-lateral border of the tergite. This passes mesiad to its insertion on the anterior border of the tergite next behind but lateral to the already described cruciform muscles. This lateral muscle passes between the anterior and posterior dorso-ventral muscles shortly to be described (Figs. 4 and 5). I will call this the *lateral oblique longitudinal* muscle. Laterally a narrow muscle strand passes dorsally between one segment and the next behind it, in a direction more or less parallel to the longitudinal body axis.

This muscle which I will call the *lateral longitudinal muscle* also passes in its course between the anterior and posterior dorso-ventral muscles (Fig. 4).

The ventral longitudinal muscles have a similar disposition except that there appears to be no counterpart to the slender lateral longitudinal muscle of the dorsal series described above (Fig. 4). Reference to Figs. 4 and 5 obviates any further description of these.

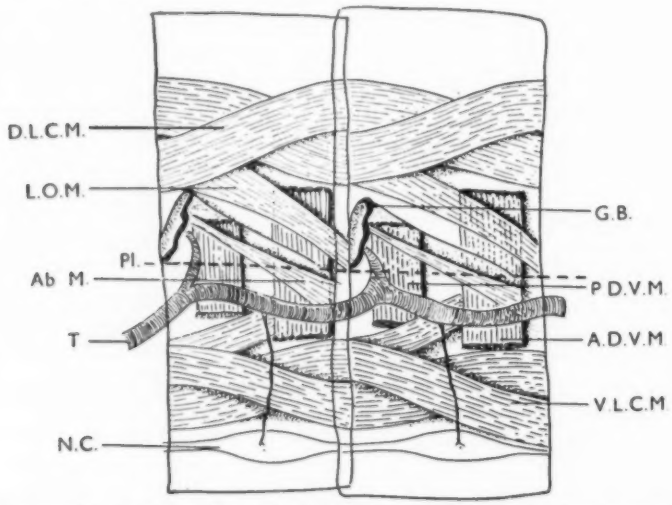

Fig. 5.—The muscles of two neighbouring gill bearing segments seen by transparency from the right side, tergal (above) and sternal (below) regions shown as if flattened out in one plane.

Ab.M. Abductor muscle ; A.D.V.M. Anterior dorso-ventral muscle ; D.L.C.M. Dorsal longitudinal cruciform muscle ; G.B. Gill base ; N.C. Nerve cord ; P.D.V.M. Posterior dorso-ventral muscle ; T. Trachea ; V.L.C.M. Ventral longitudinal cruciform muscle ; Pl. Tergo-sternal junction. (Lateral longitudinal muscle not shown).

The Dorso-ventral muscles

The dorso-ventral muscles—those passing between tergite and sternite have similarly become divided into separate units.

The first is an anterior dorso-ventral muscle, lateral to the main longitudinal muscles as well as to the longitudinal trachea of the body. It lies in the angle between the cruciform muscles and the lateral oblique longitudinal muscle (Fig. 4).

The second is a posterior muscle passing from its origin on the sternite of a segment, upwards vertically to the raised part of the body wall on which the gill is inserted. This muscle is shorter and weaker than its anterior counterpart.

The third muscle of this series passes, from its origin on the sternite antero-laterally, to its insertion on the tergite above on the outer wall of the gill base. It passes upwards and backwards in its course (Fig. 5). Because this muscle passes between sternite and tergite—however obliquely—it would appear

clearly to be a modification of the normal dorso-ventral muscle group. I will call it the abductor muscle since from its attachment to the gill base (Fig. 5) it causes the gill to turn outwards. Much of the movement of the abdomen as a whole and the gills in particular can be inferred from the disposition of the muscles.

The nymph holds itself stationary with its abdomen slightly curved upwards at its tip. It flicks itself forwards by increasing this curvature, raising and then lowering its widely spread out caudal filament in a sudden movement. Thus the thrust comes from the horizontally placed setose caudal filaments which in this first movement are moved up and down as are the tail flukes of a whale. As far as can be ascertained by direct observation or photography this is the only time when such a method of propulsion is used. Dorsal and ventral longitudinal muscles of the last segments of the abdomen bring this about.

In subsequent swimming, once the first thrust has been made, the abdomen together with its caudal filaments behaves in the piscine manner.

C. dipterum swims by rhythmical side to side movements of the body. This rhythm, produced by the cruciform muscles already described, imparts itself to the caudal filaments. The track of such movements can often be traced on a substratum of silt over which the caudal filaments move from side to side. The filaments are now held relatively close to each other and while photography has given no very clear picture of their precise attitudes in their lateral movements it appears that they are rotated on their long axis so as to present to the water at the side against which they are moving an oblique surface. This is due to an outer leading filament being at a higher level than the median and this again at a higher level than the remaining one, the setae with which they are fringed forming a semblance of a membrane. The filaments are freely flexible and it is difficult to see how they could fail to respond to the lateral rhythm imposed by the abdominal segments in front. They thus are caused to move from side to side turning as does a single oar when used for propelling a boat from the stern. We thus find that the nymph of *C. dipterum* uses both cetacean and piscine mechanisms and further that it has the ability to convert the former into the latter method of locomotion. The cruciform disposition of both dorsal and ventral muscles of the longitudinal series can easily account for the piscine method of locomotion, i.e. by rhythmical lateral waves of movement about a vertical axis passing down the body. It seems reasonable to regard the cruciform longitudinal muscles as the result of a modification of normal uncrossed segmental muscles. By the separation of these into muscles orientated in opposite directions in each segment, opposing or antagonistic muscles have been brought into being. Thus as explained diagrammatically in Fig. 7 a muscle passing medianwards from before backwards can on contraction on a fixed anterior origin move the posterior boundary of its segment to the left side. In so doing it puts its crossing antagonistic member (this passing lateralwards from before backwards) into a state of tension, stimulating this in turn to contract. The result of this is to swing the posterior boundary of the segment in the direction opposite to that already undergone i.e. from left to right. Successive segments from before backwards,

being brought in sequence under the corresponding muscle action, must therefore oscillate about a vertical axis and so with the help of the setose caudal filaments bring about forward propulsion through the water in much the same way as happens in fishes.

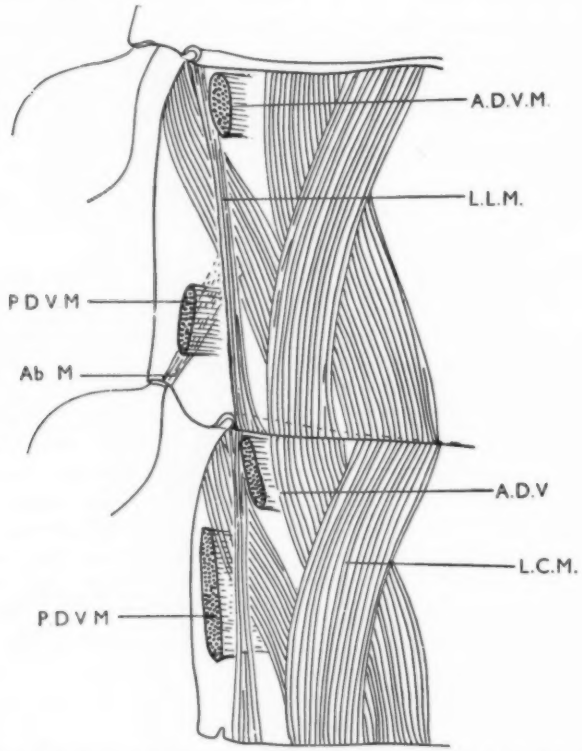

Fig. 6.—Muscles of the last gill bearing segment and the segment next behind it as seen dorsally. Ab.M. Abductor muscle ; A.D.V.M. Anterior dorso-ventral muscle ; L.L.M. Lateral longitudinal muscle ; L.C.M. Longitudinal cruciform muscle ; P.D.V.M. Posterior dorso-ventral muscle.

The majority of swimming insects propel themselves by their legs. Those that move by abdominal movements e.g. *Ephemera danica* do so by rather clumsy up and down movements about a horizontal transverse axis. Examination of the longitudinal muscles in such a case, shows no cruciform disposition.

All the other muscles would appear to have functions related to gill rather than body movement.

The insertion of each gill on its base is by way of a flexible arthrodial membrane and therefore any muscle attached to the base is able only indirectly to cause gill movements. I nevertheless propose to regard these muscles now under consideration as the direct muscles of the gills. The posterior dorso-ventral muscles depress the gill base and hence must elevate the gill. The

abductor muscle pulls on the outer border of the gill base and thus causes the gill to rotate outwards on its insertion.

The lateral oblique muscles of the longitudinal series would appear to pull indirectly on the gill base of the segment next in front (Fig. 4) and thus further assist the posterior dorso-ventral muscle to this end.

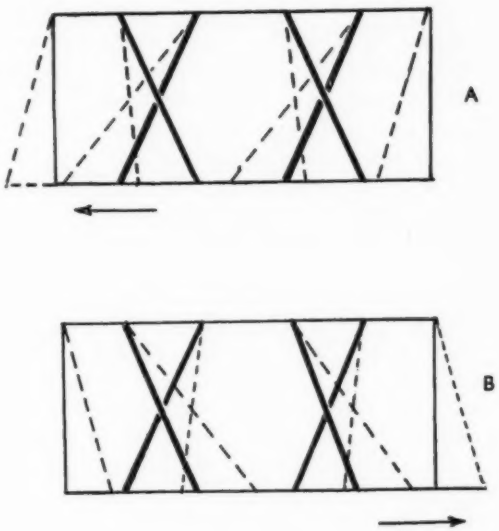

Fig. 7.—Diagram of the cruciform muscles of a segment and the effect on that segment of the contraction of one element of the cruciform series in bringing the posterior boundary of the segment A, to the left, assuming the anterior segmental border to be fixed, and B, to the right.
Before contraction : muscles and segmental boundaries in full line.
After contraction : muscles and segmental boundaries in broken line.

The disposition then of the muscles can explain much of gill movement, always having regard to the important factor of elasticity of the cuticle in the concerned regions which must account for part of the movement at the end of a muscle's contraction.

It is interesting to note that the musculature of the last gill-bearing segment (Fig. 6), differs in no appreciable manner from that of the segments immediately in front, and this in spite of the fact that these gills are immobile. On segment 8 of the abdomen (Fig. 6), there is no abductor muscle, a feature that might well be expected since no gill is present there. The posterior dorso-ventral muscle, which in gill-bearing segments is short and small, is here widely extended in its insertion and origin and is more anteriorly placed than in gill-bearing segments thus presumably concerned with normal segmental activity from which perhaps gill musculature and movement has evolved.

DISCUSSION

That the currents set up by gill movements in *Chloeon* are probably of importance only when the water is deficient in oxygen is shown by the increased activity of the gills under the latter conditions. This has also been proved by the findings of Wingfield (1939). But that they have a function to perform in irrigating the gills themselves and the body surface would seem clear from the precision of the currents set up by the gills in motion. This is further substantiated by the means whereby it is ensured that fresh water, as distinct from that already used and presumably robbed of some oxygen, is explored by gill movement. Thus the most posterior gills serve to deflect used water away from the body and prevent the setting up of vortical currents which would merely exploit the same water time after time.

That water from all surrounding regions is explored by the currents set up seems adequately to reflect the pelagic habit of the animal. For though most of it passes over the animal from above and in front of the body, other currents supply the gills from below the body level at each side and from behind.

The question of the homology of gills with other structures depends largely on musculature. Börner (1908) regards gills as homologous with true limbs since they appear to arise embryologically in much the same way as do the legs. The embryonic buds on the abdomen which are serially homologous with those destined to form appendages on the head and thorax, become converted in Ephemeroptera into gills. Arguing from this point Börner (1908) proceeds to homologise the dorso-ventral gill muscle (elevator) with the subcoxal muscle of the thoracic limb and the direct rotatory (abductor) muscles with the coxotergal and coxo-subcoxal muscles.

Börner however refuses to homologise tracheal gills with wings as does also Dürken (1907) on grounds of musculature though he disagrees with Dürken in that the latter author regards gills as of tergal origin.

On grounds of pure morphology as distinct from development, the gills of *Chloeon* do appear to be tergal structures and without going so far as to homologise gills with wings as was suggested by Gegenbaur (1878) and Heymons (1896), there would seem to be good grounds for regarding the musculature of the lateral regions of the gill-bearing abdominal segments as evolutions of the longitudinal and dorso-ventral muscles of an unmodified body segment, analogous to the muscle changes which have occurred in wing-bearing segments of the thorax.

The cruciform arrangement of the longitudinal muscles of the abdomen is peculiar and would appear to be a caenogenetic adaptation subserving the purpose of locomotion in an animal which has become an expert swimmer using its abdomen rather than its limbs as is more usual in aquatic insects.

SUMMARY

1. The nymph of *Chloeon dipterum* is a pelagic animal living in ponds. Its plate-like bilamellate gills are described.

2. By means of metachronal rhythmical movements of the gills, in which members of pairs beat synchronously, currents of water are set up over the

body. These currents which are on the whole axial to the body explore water from all regions surrounding the body.

3. The gill and abdominal musculature is described and it is shown that a modification of normal musculature has occurred to provide direct muscles to the gill bases and also to make possible the habit of swimming by rhythmical movements of the abdomen rather than by limbs. These movements are lateral and are made about a vertical axis. Swimming is always preceded by a vigorous up and down movement of the caudal filaments. This movement about a transverse axis as in the tail flukes of a whale is then abandoned as the side to side movements of the abdomen take charge, when the animal swims as does a fish.

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THE MULTIMAMMATE MOUSE *RATTUS* (*MASTOMYS*) *NATALENSIS* SMITH : A LABORATORY-ADAPTED AFRICAN WILD RODENT

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(With 1 plate)

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INTRODUCTION

The joint Plague Research Laboratory of the Union Health Department and the South African Institute for Medical Research has maintained a laboratory breeding stock of multimammate mice since 1939. The nucleus was first established at a plague research camp in the Orange Free State from animals sent from the Glen Grey district, Eastern Cape Province by the late Dr L. Fourie, to one of us (D.H.S.D.). A stock from Rooiwal, O.F.S., was started early in 1940 and three lines were developed : Transkei, Rooiwal and a cross between them. From 1940 onwards this stock was used in experimental and routine work on plague (Union of S. Africa, 1941).

In 1946 the original stock was superseded by seventeen wild pairs from Baragwanath, ten miles south-west of Johannesburg, kindly obtained by Mr N. J. Smith, then of the Johannesburg City Health Department. Four members of the original Rooiwal/Transkei stock were retained, however, and it is possible that, despite precautions, some interbreeding with the Johannesburg animals may have taken place. The Johannesburg stock was not inbred and is still maintained at this Institute. Breeding stocks have been established in Washington (Army Medical Graduate School) in 1950 and in London (Zoological Society of London) in 1952. Owing to the similarity of much of

western U.S.A. to the semi-arid regions of southern Africa in which multimammate mice thrive, it was agreed to keep them in the east because of the danger of their escaping and occupying the same niche in plague epidemiology in the plague-enzootic regions of western U.S.A. as they do in Africa. Such a development would immeasurably worsen the plague potential as regards carriage of infection to man in that area, on account of the well-known semi-domestic habits of multimammate mice which link the wild rodent reservoir with human habitations (Davis, 1953).

Stocks of multimammate mice from the London Zoo nucleus have been distributed to various laboratories in Great Britain, amongst which are the National Institute for Medical Research, the London School of Hygiene and Tropical Medicine, the Institute of Animal Genetics in Edinburgh and the Christie Hospital in Manchester. Stringent precautions to prevent escapes have been taken in Great Britain.

BIOLOGICAL DATA

Records of the reproductive performance, length of life and other life history data have been kept of all breeding animals ; in general the methods were those developed by Ranson (1934) for the colony of voles (*Microtus agrestis*) established and maintained at the Bureau of Animal Population, Oxford, with which one of us (D.H.S.D.) was familiar. Oliff (1953) made a study of the fertility of the laboratory-bred multimammate mouse stock, based on records of the colony between 1946 and 1949. At the same time Helen Johnston & Oliff (1954) made a study of the oestrus cycle.

In captivity, multimammate mice are not so easily handled as white mice, and little difference in aggressive behaviour could be detected for the first six years of their domestication. It was hoped that an albino mutant would appear that might be tamer than the wild type. Albino multimammate mice are known in the Belgian Congo, and true melanic forms from Uganda. One albino female, sent to us by Dr R. Devignat from the Belgian Congo, was kept with a series of local males but never bred. In 1953 a " dilute " red-eyed mutant appeared, and is now manifestly tamer than the wild type. The genetic constitution is being studied in greater detail, in association with Dr D. J. Nolte of the Zoology Department of the University of the Witwatersrand. It is pertinent here to note that Hatt (1940), referring to the multimammate mouse of the Belgian Congo, remarks that it should make an ideal laboratory animal on account of its local variability, ready availability, hardihood in captivity and high birth rate—qualities which have been fully confirmed by our experience.

IMPORTANCE IN MEDICAL RESEARCH

Up till 1953 the chief use that multimammate mice were put to in this laboratory was as test animals for plague. Many plague laboratories use Swiss white mice, but at the South African Institute for Medical Research multimammate mice were found more satisfactory on account of their greater hardiness and high, uniform susceptibility to plague in comparison with the SAIMR stock of white mice then available (Union of S. Africa, 1941 and

Amies, 1951). Since 1953 the multimammate mouse has assumed special importance in two further respects : one of us discovered that about half the females and somewhat fewer males dying from natural causes were suffering from spontaneous adenocarcinoma of the glandular stomach (Oettlé, 1955)—a tumour which is exceedingly rare in species other than man (Stewart, 1953) ; in addition, the multimammate mouse has recently been shown to be exceptionally susceptible to experimental infection with *Schistosoma mansoni* (Lurie & de Meillon, 1956), even more so than the white mouse.*

The multimammate mouse has thus come to the fore as a laboratory animal, and for this reason we bring together here (Table 1) some of its characteristics and the extent to which it shares them with laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*).

TAXONOMIC STATUS

The multimammate mouse is distributed from the eastern Cape Province throughout Africa south of the Sahara and to Morocco in the far north-west. The species is divided into a large number of geographical races, but although it is variable in colour it is remarkably uniform in size. There is for example little difference in the body-weight range of multimammate mice in Sierra Leone (Brambell & Davis, 1941) and Johannesburg (Oliff, 1953). Both races become sexually mature at about 40g. body-weight and few are found weighing over 100g. in the wild.

The current valid name for the multimammate mouse is *Rattus* (*Mastomys*) *natalensis* A. Smith 1834 (Ellerman & Morrison-Scott, 1953). It was known by the specific name of *coucha* A. Smith, 1836, until Roberts (1944) pointed out that Smith had described the same species twice, thus the earlier name has priority.

There is at present a difference of opinion as to whether the multimammate mouse should be grouped with the ' rats ' (Genus *Rattus* Fischer) or with the ' mice ' (Genus *Mus* Linnaeus) or whether it should remain as a separate genus *Mastomys* Thomas. Thomas (1915) divided the African ' rats ' into a number of subgenera, amongst which was *Mastomys*. This subdivision was based on the mammary formula, but Thomas never, apparently, provided his promised diagnosis of his subgenus *Mastomys*, although he dealt with some of the others and raised them to generic rank. Following upon publication of a key to African Rodentia by St. Leger (1931) the multimammate mouse was given generic rank until Ellerman (1941) listed it as a subgenus of *Rattus*. He noted however that the molars were reminiscent of the *Mus* type and suggested that it " may be one of the primitive lines that may have given rise to *Mus* on the one hand, or part of *Rattus* on the other ". (p, 169). In a recent study of the affinities of some South African Murinae, Lundholm (1955) concluded that *Mastomys* should be accepted as a full genus and mentioned

* Certain other uses for this species have been reported from other laboratories. Bouilliez in 1917 showed that "*Mus coucha*" was susceptible to *Leishmania donovani*, and Vincke *et al.* (1953) that it would succumb to *Plasmodium berghei*. These findings have been confirmed by Gunders (1956), who also demonstrated its susceptibility to *Babesia rodhaini* and *Trypanosoma congolense*.

distinctive characters in the teeth, ear ossicles, cranial bones and cranial features. He did not compare *Mastomys* with *Mus*. Such a comparison shows that the two share the following characters : three-rooted upper first molars, forked mastoid processes of squamosal, and weak supraorbital ridges

TABLE 1.

Comparison of the multimammate mouse with the laboratory rat and mouse

	Rattus (*Mastomys*) *natalensis*	*Rattus norvegicus*	*Mus musculus*
A. RESEMBLING THE RAT			
Subapical notch on inner surface of upper incisors	absent	absent (Miller, 1912)	present (Miller, 1912)
Gall-bladder	absent	absent (Greene, 1935)	present (Fekete, 1941)
Odour of urine	negligible	negligible	musty
Eye colour in dilute agouti mutants	ruby	ruby	black
B. RESEMBLING THE MOUSE			
Posterior process of squamosal	forked with strut (Lundholm, 1955)	hookshaped undivided (Greene, 1935)	forked with strut
Roots to M.*1*	three (St. Leger, 1931)	five (Miller, 1912)	three (Miller, 1912)
Concentration of ^{131}I in submandibular gland	2·75–4·1	0·44 (Cohen)	4·7 (Cohen)
Alkaline phosphatase in neutrophile leucocytes	absent	present	absent
C. INTERMEDIATE			
Arrangement of tubercles t1, t2 and t3 in M.*1*	t1 moderately backwardly displaced (Hill & Carter, 1941)	crescentic	t1 backwardly displaced (Miller, 1912)
Reduction of M.3	moderately or strongly reduced (Ellerman, 1941)	not reduced (Miller, 1912)	strongly reduced (Miller, 1912)
Supraorbital ridges	weak (Hill & Carter, 1941) but developing with age	strong (Donaldson, 1924)	weak (Miller, 1912)
Body weight at sexual maturity	40g (Oliff, 1953 ; Brambell & Davis, 1941)	120g (Donaldson, 1924)	15g (Engle & Rosaco, 1927)
D. DISTINCTIVE			
Posterior nares	narrow (St. Leger, 1931)	broad (Miller, 1912)	moderate (Miller, 1912)
Anterior process of baculum (os penis)	cordate (Lazer)	oval (Lazer)	lanceolate (Lazer)
Mammary formula	14 or more (Thomas, 1915)	3–3=12 (Donaldson, 1924)	3–2=10 (Miller, 1912)
Female prostate	present (Brambell & Davis, 1941)	absent Brambell & Davis, 1941)	absent (Brambell & Davis, 1941)
Preputial gland	absent	present (Miller, 1912)	present (Greene, 1935)
Chromosome number (2N)	36 (Matthey, 1954)	42 (Painter, 1926)	40 (Painter, 1926)
Age at first oestrus	104 days* (Johnston & Oliff, 1954)	77 days (Donaldson, 1924)	39–53 days (Mirskaia & Crew, 1930)
Duration of oestrus	6–7 days (Johnston & Oliff, 1954)	4 (Fekete, 1941)	5 (Mirskaia & Crew, 1930)

* Some are as early as 70 days.

(at least in younger animals). The moderate backward displacement of tl. in M.*1* in *Mastomys* is a step towards the marked displacement of this tubercle in *Mus* (Hill & Carter, 1941). The subapical notch to the upper incisor in *Mus*—which is one of the generic characters employed for separating *Mus* from *Rattus*—is not found in *Mastomys*.

Two biochemical similarities to the mouse have recently been demonstrated by one of us (A.G.O.). The first is its ability to concentrate ^{131}I in the submandibular glands, a function which Cohen, Logothetopoulos & Myant (1955) first discovered in the hamster. The experiment was performed on *Mastomys* with Dr Cohen's assistance. About 50 microcuries of ^{131}I as sodium iodide in normal saline was injected intraperitoneally into each of three male and one female laboratory-bred multimammate mice. After approximately one hour, a blood sample was taken, and the left submandibular gland removed, separated from the major sublingual gland, and digested in 15 per cent potassium hydroxide. The ratio of gland radio-activity to that of the blood plasma was 3·1, 3·2 and 4·1 in the males, and 2·75 in the female. This is much higher than is found in the rat (Cohen). The second feature of similarity is the absence of alkaline phosphatase from the neutrophile leucocytes of both mice and multimammate mice, using the α naphthyl phosphate technique for this enzyme (Pearse, 1953). Alkaline phosphatase is easily demonstrable in rat neutrophile leucocyte cytoplasm (Wachstein, 1946).

The other characters listed in Table 1 do not call for detailed comment. Unique features in the multimammate mouse are the well developed female prostate glands and the large number of mammae arranged in a series along the flanks from the pectoral to the inguinal region. Eight to ten pairs are the rule, but this number is sometimes exceeded.

The actual taxonomic status of the multimammate mouse will take time to resolve, but for the present, pending a detailed revision, we follow current nomenclatural usage and retain *Mastomys* as a subgenus of *Rattus*. This is another case in which the vernacular name is of more practical use than a scientific name which is not fully established.

ACKNOWLEDGMENTS

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Summary

1. Laboratory-breeding stocks of the multimammate mouse, *Rattus* (*Mastomys*) *natalensis*, have been maintained since 1939 and have become of increasing importance in medical research. This mouse has been used primarily as the standard test-animal in routine diagnostic and experimental work in plague.

2. It is highly susceptible to experimental infection with *Schistosoma mansoni*, and in consequence has assumed importance in bilharzia research.

3. A high proportion (30 to 50 per cent) of animals dying in the colony from natural causes have been found to be suffering from spontaneous adenocarcinoma of the glandular stomach—a condition which is extremely rare in animals other than man. The multimammate mouse promises to be an important experimental animal in cancer research.

4. The taxonomic status of the multimammate mouse has not been satisfactorily defined. Some of its anatomical and physiological features are *Rattus*—like, others *Mus*—like, while others appear to be unique (e.g. the presence of a prostate gland in the female).

5. The known similarities and differences between the multimammate mouse, the laboratory rat and the laboratory mouse are tabulated. On the available data it is hard to say whether it should be classified as a subgenus of *Rattus*, as it is at present, or whether *Mastomys* should be given generic rank or made a subgenus of *Mus*.

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A pair of multimammate mice, *Rattus* (*Mastomys*) *natalensis*. The female is on the left and has just warded off an advance from the male

Photo. A. Veenstra

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Note added in proof:

Since this paper was submitted for publication three papers have come to our notice which deserve mention. H. W. Setzer ('Mammals of the Anglo-Egyptian Sudan'. Proc. U.S. Nat. Mus. **106,** 447, 1956), and F. Petter ('Remarques sur la systématique des *Rattus* Africains . . . ' Mammalia, **21,** 125. 1957) discuss the taxonomic status of African *Rattus*-like species (including *Mastomys*). Their concern over the inadequacies of the present nomenclature leads us to hope that collaborative effort will resolve the problem sooner than was anticipated. Petter accepts *Mastomys* as a subgenus, and has grounds for thinking that there may be two species living together in West Africa. Setzer retains *Mastomys* as a genus, and notes that two *Mastomys* species occur together in parts of the Sudan.

P. L. Pirlot ('Croissance et maturité sexuelle chez *Mastomys coucha* Smith'. Mammalia, **21**, 385. 1957) discusses the body-weight distribution of a wild population from Elisabethville, Belgian Congo. A median body-weight of 39·7 g. (limits 30·0–52·6) for males was calculated (using probits), based upon the body-weights of animals showing spermatozoa in the cauda epididymis. The mean body-weight of the adult *Mastomys* population sample is given as 45·15 g. for males and 43·82 g. for females. The median body-weight of females (not given) would not be much less than that for the males, thus it is seen that female *Mastomys* in the Belgian Congo attain sexual maturity at approximately the same body-weight, namely 40 g. (if due allowance be made for the different methods of calculation) as they do in South Africa and Sierra Leone (see Table I, above, in text).

COPEPODA PARASITIC ON BRITISH AMPHIPODA (CRUSTACEA), WITH A DESCRIPTION OF A NEW SPECIES OF *SPHAERONELLA*

BY

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[Accepted 11th February 1958]

(With 26 figures in the text)

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INTRODUCTION

In July 1957 a parasitic copepod was found in the brood pouch of the amphipod *Erichthonius brasiliensis* (Dana) at Plymouth. While the systematic position of this copepod was being investigated, Dr J. P. Harding suggested that I should also examine the unnamed copepods found as parasites on amphipods in the collection at the British Museum (Natural History). This paper is a report on this examination.

MATERIAL

Two specimens were obtained from Plymouth.

A single specimen, from the Norfolk coast was received from Mr R. Hamond.

The British Museum material was in seven tubes. One tube, from the Norman collection, contained five species of amphipods. Four of the specimens were infected with copepods, while the fifth, *Perioculodes longimanus* (Bate & Westwood) was not infected, but had several abnormally large eggs in its brood pouch. One of the specimens in the tube had lost most of its appendages, making determination by ordinary methods difficult. This specimen was sent to Mr G. M. Spooner, who determined it as a female *Aora typica* Kroyer. The remaining tubes each contained a single host species, or copepods collected from a single host species.

Family HERPYLLOBIIDAE

Rhizorhina ampeliscae Hansen, 1892

Material examined. (1) One adult female from the brood pouch of *Ampelisca diadema* (Costa), Guernsey 1906 (Norman Collection). (2) Two adult females and a male from *Ampelisca brevicornis* (Costa), Garroch Head, Clyde area, July 1954 ; collected by Dr R. B. Pike.

These appear to be the only records of this species since Hansen's (1892) original description. Leigh-Sharpe (1926), in his account of the Herpyllobiidae, gave figures of this species, taken from Hansens original drawings. The copy of the male is inaccurate ; the setae on the second abdominal segment have been omitted, and the large flattened aesthetasc on the first antenna is shown as being terminal, resembling a podomere. These mistakes have been reproduced by Oorde-de-Lint and Schuurmans Stekhoven (1936). The abdominal setae were correctly figured by Hansen, and he also showed the aesthetasc in its correct position, coming from the middle of the third podomere.

Distribution. Norway, Denmark (Hansen) ; now recorded from the Clyde and Guernsey.

Hosts. *Ampelisca brevicornis* (Costa) (Hansen, as *A. laevigata*, and present paper), *A. diadema* (Costa) (present paper).

Family CHONIOSTOMATIDAE

Sphaeronella leuckarti Salensky, 1868

Syn. *S. elegantula* Hansen, 1897.
? *S. aorae* Scott, 1905.

Material examined. (1) One adult female and two pupae on *Cheirocratus sundevalli* (Rathke), E. Little Cumbrae Island, Clyde, 4–6 m. August 1954. Collected by Dr R. B. Pike. (2) One adult female and one male on *Aora typica* Kröyer, Guernsey 1906 (Norman Collection).

When Hansen wrote his monograph (1897) he described eight species of the *leuckarti* group of *Sphaeronella*, and said ' I must consider *Sphaer. Leuckarti* Sal. as a ninth (to me unknown) species '.

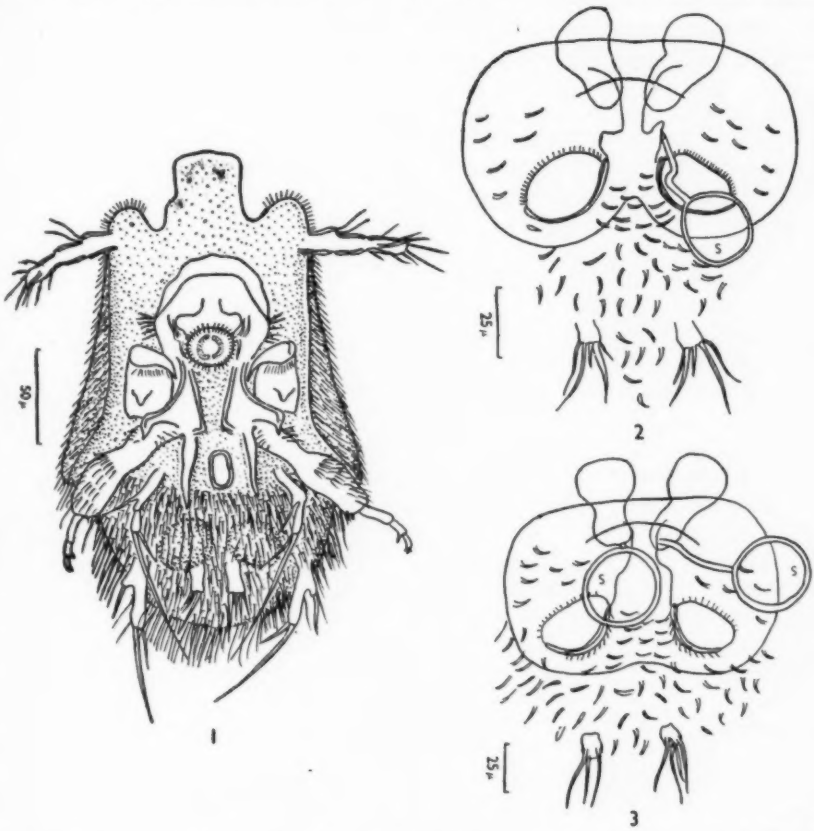
The specimens from *Cheirocratus sundevalli* were at first identified as *Sphaeronella elegantula* ; they agreed in detail with Hansen's description. When the specimens from *Aora typica* were examined they were also found to agree with the description of *S. elegantula*. *Aora* belongs to the same family as *Microdeutopus*, from which Salensky described *S. leuckarti*, and when Salensky's figures were examined it became evident that *elegantula* is a synonym of *leuckarti*.

This synonymy is being based primarily on the males, which are more characteristic than the females. The points in common between Hansen's description of *elegantula*, Salensky's description of *leuckarti*, and the male which I have examined (Fig. 1) are as follows.

All have the characters of the *leuckarti* group as given by Hansen, and in addition the following detailed similarities.

The sub-median skeleton is produced backwards behind the base of the maxilla to form a short spike over the outer edge of the base of the maxillipede. The processes at the inner margins of the bases of the maxillipedes are very large, and there is an irregular ring-like structure between them. There is a distinct triangular projection on the basal podomere of the maxilla. The caudal rami are longer than broad, and have about four terminal setae. These characters will serve to distinguish the male of *leuckarti* from any other species in its group.

The females described by Hansen and Salensky agree in shape and size, and in the general form of the genital area. There is some variation in the degree of concavity of the posterior border of this area. Hansen figures a specimen in which this border is almost straight, but says that in another specimen the border was slightly more concave. The specimen figured by Salensky had a posterior border similar to that of the female from *Aora* (Fig. 2).

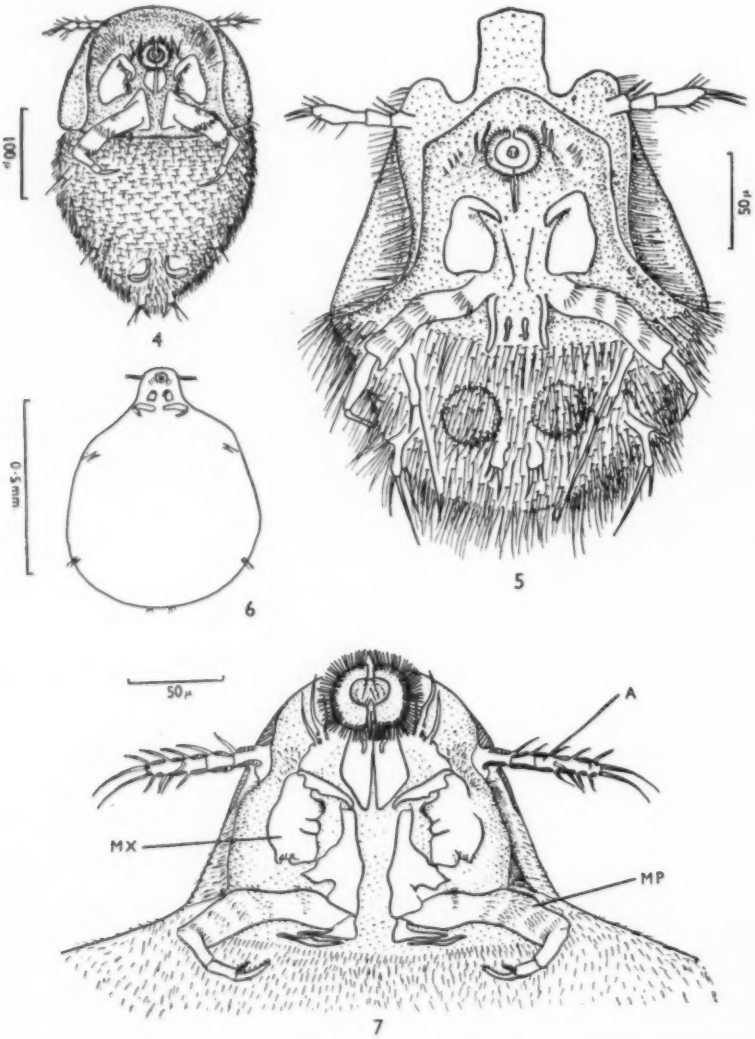


Figs. 1–3.—*Sphaeronella leuckarti*. 1, male, ventral view. 2, genital area of female from *Aora typica*. 3, genital area of female from *Cheirocratus sundevalli*. s–spermatophores.

The female from *Cheirocratus* (Fig. 3) had a less concave border. Both females examined by me had a number of peculiar membranous hairs on and behind the genital area ; similar hairs were described by Hansen from one of his specimens. Both Hansen and Salensky figure only two setae on the caudal rami of the female. Figs. 2 and 3 show that four or even five terminal setae may be present. This brings the caudal ramus of the female into line with that of the male. However, these setae are easily broken off, and the rami may present a very different appearance.

Scott (1905) described *Sphaeronella aorae* from '*Aora gracila* (Bate)'. This is probably a synonym of *leuckarti*; it is certainly a member of the *leuckarti* group, but the figures and description are quite inadequate to decide which species it should be assigned to.

Distribution. Naples (Salensky), Denmark (Hansen). Now recorded from the Clyde and Guernsey.



Figs. 4–7.—*Sphaeronella danica.*—4, young female, ventral view. 5, male, ventral view. 6, female, ventral view. 7, head of female, ventral view, A–antennule; MX–maxilla; MP–maxillipede.

Hosts. *Microdeutopus gryllotalpa* Costa (Salensky), *Cheirocratus sundevalli* (Rathke) (Hansen and present paper), *Aora typica* Kröyer (present paper).

Sphaeronella danica Hansen, 1897

Material examined. (1) Two adult females, one very young female, one male and a pupa from the brood pouch of *Corophium crassicorne* Bruzelius, Guernsey 1906 (Norman Collection). (2) Two females, one of which has fully developed larvae in its egg sacs, from brood pouches of *Erichthonius brasiliensis* (Dana), Asia Shoal, Plymouth, July 1957.

The adult female from *Corophium crassicorne* was quite typical of the species, agreeing with Hansen's original description in most details. The only exception was a detail of the genital area, which is discussed later. Fig. 4 shows a very young female, which contrasts greatly with the adult. The male (Fig. 5) was not figured by Hansen. The only differences which Hansen gives from the male of *elegantula* (*leuckarti* Salensky in this paper) are the more clumsy shape and the slightly shorter caudal stylets. There are certain other differences. The processes at the bases of the maxillipedes are shorter and weaker in *danica*, and there is a pair of projections between these, instead of the ring-like structure which is present in *leuckarti*. The maxillule lacks a posteriorly directed process, and there is no spine formed on the outer side of the base of the maxillipede.

The females from *Erichthonius brasiliensis* may be described as follows. The body is sub-globular, with a well defined head (Figs. 6 and 7). The length is about 0·7 mm. and the maximum width 0·52 mm. In life the body was coloured orange.

The antennules have two sub-equal basal podomeres and a much longer distal podomere. Eleven setae are present on the whole antennule, the terminal pair being the longest.

The rostrum is of the usual pattern for the genus, with moderately long setae around the border.

The antennae could not be found.

The maxillules have three forwardly directed branches, but no posteriorly directed branch (Fig. 8).

The maxilla is well developed, and the maxillipede normal for the genus with groups of fine hairs on the basal podomore. The terminal spine is finely spinulated. Two pairs of trunk appendages are present ; each is a single podomere with two terminal setae.

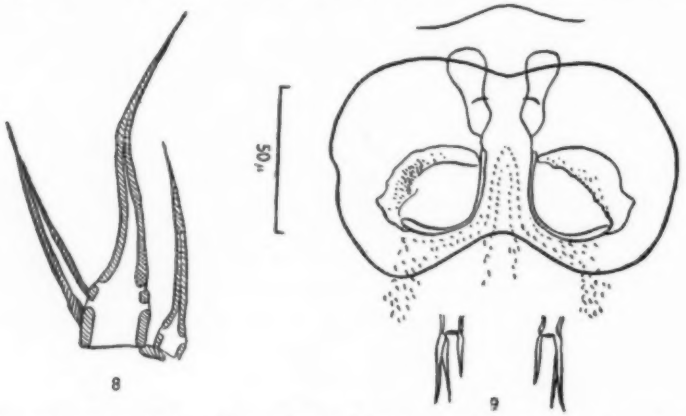
The genital area (Fig. 9) is wider than long, slightly concave anteriorly and more strongly concave posteriorly. The genital openings are curved. There is a scattered pattern of minute hairs on the posterior part of the area. Some of the hairs extend beyond the area as far back as the caudal rami. The paired receptacula seminis extend from the anterior edge of the genital openings to a short way in front of the genital area.

The caudal rami lie behind the genital area ; each is provided with three setae.

A spermatophore was found attached to one female. The body of the spermatophore was 38 μ long, and the stalk was 46 μ long.

The ovisacs are oval, measuring about 0·66 × 0·58 mm. One female had six ovisacs, each of which contained 70 to 80 eggs.

The above description differs in some slight details from that given by Hansen, but I believe that the specimens belong to his species, for the following reasons. The body is of the same size and shape, and the maxillules lack a posteriorly directed process. This was also the case in the undoubted female



Figs. 8–9.—*Sphaeronella danica*. 8, maxillule of female, greatly enlarged. 9, genital area of female.

danica from *Corophium crassicorne*. The genital area agrees with Hansen's description in all particulars except one. Hansen's figure shows the hind border projecting backwards in the middle. I believe this to be an error. Fig. 9 shows that the minute hairs on the posterior part of the genital area continue backwards in two series, and this might easily give the impression of the genital area projecting backwards between them.

The larva of *S. danica* was not described by Hansen. Fully developed larvae were found in the egg sacs of one of the females from *Erichthonius*. The general form of the body is shown in Figs. 10 and 11.

The antennules have three podomeres, the last with two strong and very long setae (Fig. 12).

The antennae have three distinct podomeres armed with minute setae, and two larger terminal setae.

The maxilla has a large basal podomere similar to that of the adult, but a terminal claw is clearly demarcated from the terminal podomere.

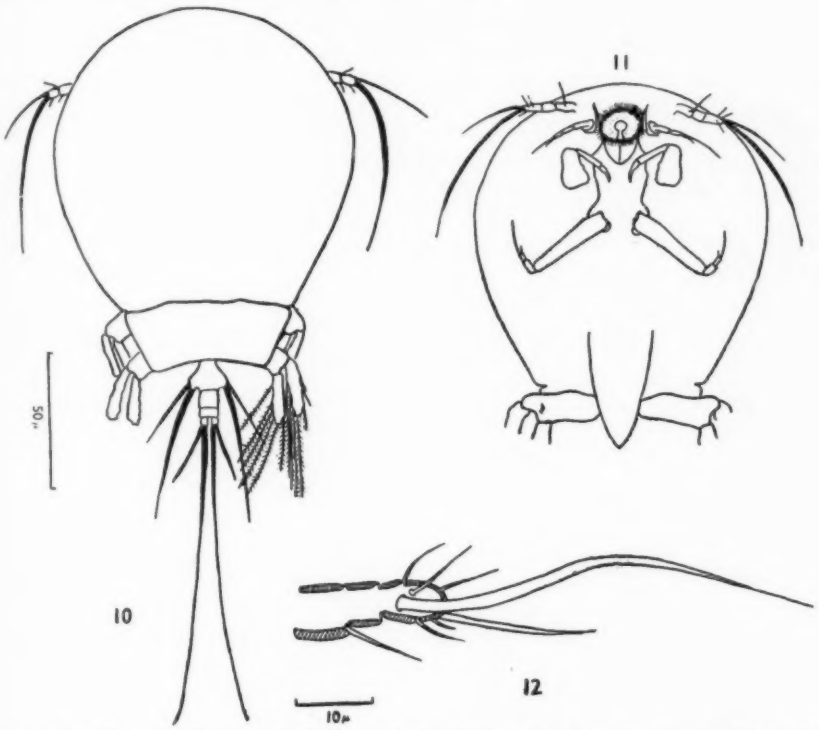
The maxillipede has a long basal podomere, followed by a smaller podomere and a terminal spine.

The two legs are well developed, the endopod and exopod of each consist of a single podomere armed with plumose setae.

The abdomen is armed with thick spiniform setae ; the stronger setae on the first abdominal segment reach beyond the tips of the weaker setae on the caudal rami. The caudal rami are about as long as wide, with two terminal setae, one of which is much longer than the other.

Distribution. Denmark (Hansen). Now recorded from Guernsey and Plymouth.

Hosts. Corophium crassicorne Bruzelius (Hansen and present paper), *Erichthonius brasiliensis* (Dana) (present paper).



Figs. 10–12.—Larva of *Sphaeronella danica*. 10, dorsal view, setae have been omitted from the legs on the left side. 11, ventral view of anterior end. 12, antennule.

Sphaeronella longipes Hansen, 1897.

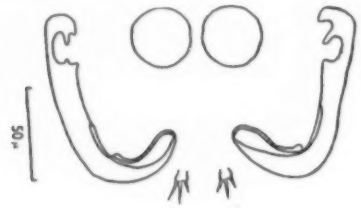
Material examined. (1) One adult female, one very young female, one male and a larva, from *Ampelisca tenuicornis* Lilljeborg, St. Brelades Bay, Jersey, 1 fthm, August 1955. Collected by Dr R. B. Pike.

The principal diagnostic character of this species is the very long terminal seta on the trunk legs of the female.

Hansen was unable to give any information about the genital area ; this is shown in Fig. 13.

A very small female is shown in Fig 14 ; this is smaller than any found by Hansen, and shows certain differences in the relative widths of the head and trunk when compared with Hansen's small females. These differences can be explained by the allometric growth of the trunk during increase in size of the female.

The male was unknown to Hansen. The specimen found during the present investigation is shown in Fig. 15. The length was 180 μ. The antennules have three podomeres, the basal one with three terminal setae, and the third with a distinct aesthetasc and six or seven setae. The antenna is distinct, with three small podomeres. The maxillule has only two forwardly directed processes. The maxilla has a series of blunt teeth and two larger protuberances on the basal podomere. The maxillipedes are of normal pattern, with stiff setae on the basal podomere. The processes from the sub-median skeleton which project over the bases of the maxillipedes are rectangular in shape, with truncated ends. This appears to be a good diagnostic character for the male of this species. The trunk legs are small ; the first has an outer branch with a stout terminal seta, and an inner branch with one large and three small terminal setae. The second trunk limb is unbranched and has three terminal setae. The caudal rami are elongated and have four terminal setae, one of which is complex.



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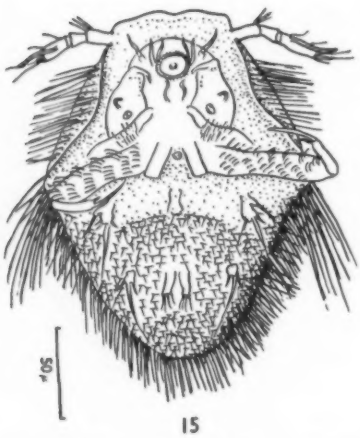

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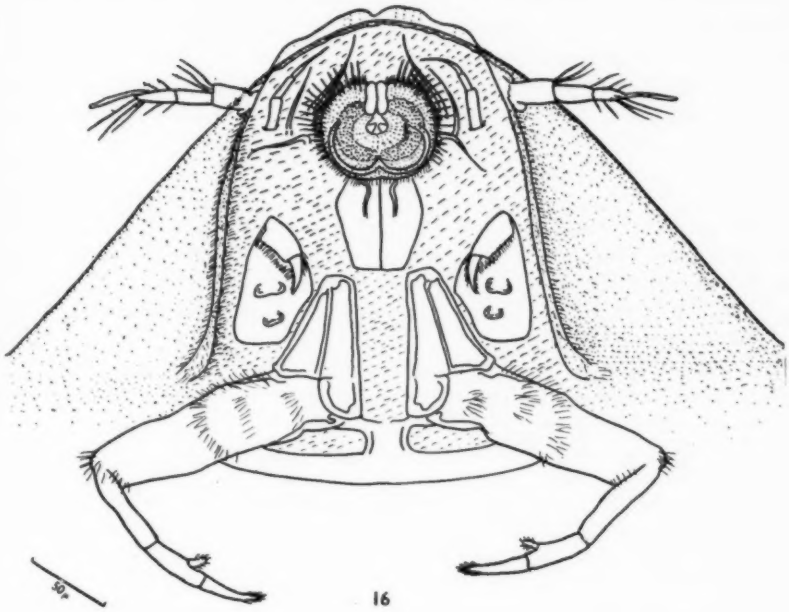
Figs. 13–15.—*Sphaeronella longipes*. 13, genital area of female. 14, very young female, ventral view. 15, male, ventral view.

Distribution. Denmark (Hansen), now recorded from Jersey.

Host. *Ampelisca tenuicornis* Lilljeborg (Hansen and present paper).



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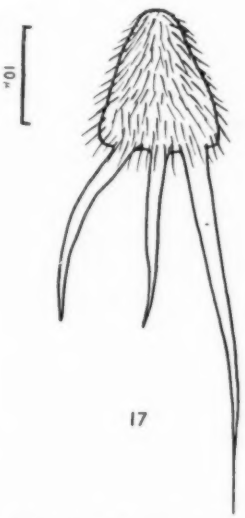

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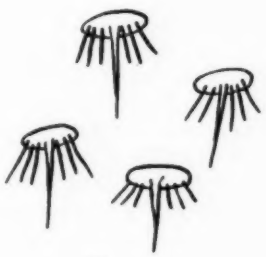

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Figs. 16–18.—*Sphaeronella frontalis*. 16, head of a large female, ventral view, showing appearance when the frontal cup is reflected dorsally. 17, first trunk limb. 18, detail of body hairs of male.

Sphaeronella frontalis Hansen, 1897

Material examined. (1) One adult female from *Ampelisca tenuicornis* Lilljeborg, Garroch Head, Clyde, 70 fthms., March 1949. (2) One adult female, with nine egg sacs, from *A. tenuicornis*, Garroch Head, 70 fthms., January 1950. (3) Three adult females and two males, from *Ampelisca macrocephala* Lilljeborg, Garroch Head 110 m., February 1950. All the specimens were collected, and the hosts determined by Dr R. B. Pike.

Some of the large females were difficult to determine at first, because the characteristic flat cup on the frontal margin was not visible from the ventral surface (Fig. 16). Once it was realised that this cup is sometimes reflected dorsally the determination was simplified. Fig. 16 is also shows the strongly developed ventral skeleton and the well marked transverse bar behind the maxillipedes. Hansen states that the trunk legs are ' normal for the genus ' ; this might be taken to mean that they have two terminal setae. All the specimens which I have examined had three terminal setae and a covering of fine hairs (Fig. 17).

The male has a characteristic covering of multiple hairs. Hansen says that each of these hairs has about ten processes springing from the base, but in my specimens there were only six or seven, and the median process was longer and stronger than the others (Fig. 18).

Distribution. Denmark (Hansen), now recorded from the Clyde.

Hosts. Ampelisca macrocephala Lilljeborg (Hansen and present paper), *A. tenuicornis* Lilljeborg (present paper).

SPHAERONELLA PIKEI, sp. n.

Material examined. One adult female from the brood pouch of *Pontocrates arenarius* (Bate), Guernsey 1906 (Norman Collection).

This species is named after Dr R. B. Pike, in recognition of his industry in collecting so many of the specimens described in this paper. The shape of the body is shown in Fig. 19. The length is 0·82 mm. The head is relatively very small. There is a fringe of fine hairs along the frontal border, and a few very small hairs on the lateral borders.

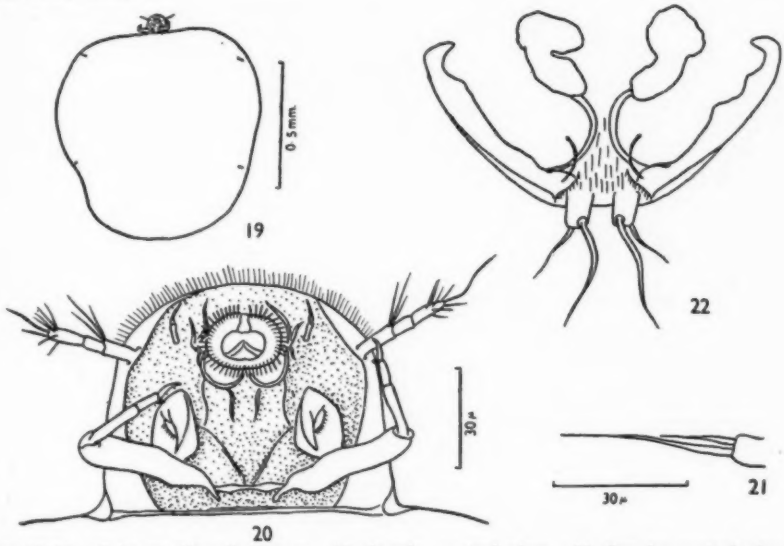
The antennule has three podomeres, with a total of twelve setae, four of which are on the basal podomere, and the remainder on the distal podomere. The antennae are small, but distinct, with three podomers. The mouth cone is normal for the genus, and the maxillules each have three processes, one of which is directed posteriorly. The maxilla has a sub-triangular basal podomere with a crescentic flap bearing a row of short hairs. The distal podomere and claw of the maxilla are fused. The maxillipedes have an elongated basal podomere, with two slender distal podomeres and a terminal spine. The ventral skeleton of the head is weakly developed, but there is a thickened ridge running transversely between the bases of the maxillipedes and a narrow bar separating the head from the trunk.

The trunk is devoid of hairs. The trunk legs are minute (Fig. 21) ; each consists of a single podomere with two terminal setae, one of which is twice as long as the other.

The genital area is triangular in shape (Fig. 22), with the caudal rami inserted within the posterior margin. The caudal rami bear two setae, one twice as long as the other.

Two egg sacs were found with the specimen ; they were oval in shape, measuring 0·48 × 0·34 mm.

The holotype is in the British Museum (Natural History) registered number B.M. 1958.1.2.4.



Figs. 19–22.—*Sphaeronella pikei* sp. n. 19, female, ventral view. 20, female, ventral view of head. 21, second trunk limb of female. 22, genital area of female.

This species is fairly closely allied to *S. giardi* Hansen and *S. bonnieri* Hansen ; in Hansen's key (1897) to the genus it would run down to *S. bonnieri*. However, it differs from *S. bonnieri* in the shape of the genital area, and in the presence of a distinct fringe of hairs along the frontal border. The trunk legs are also unusual, having one seta much longer than the other. This is a similarity to *S. longipes*, but the latter species has much larger trunk legs, and a very different genital area.

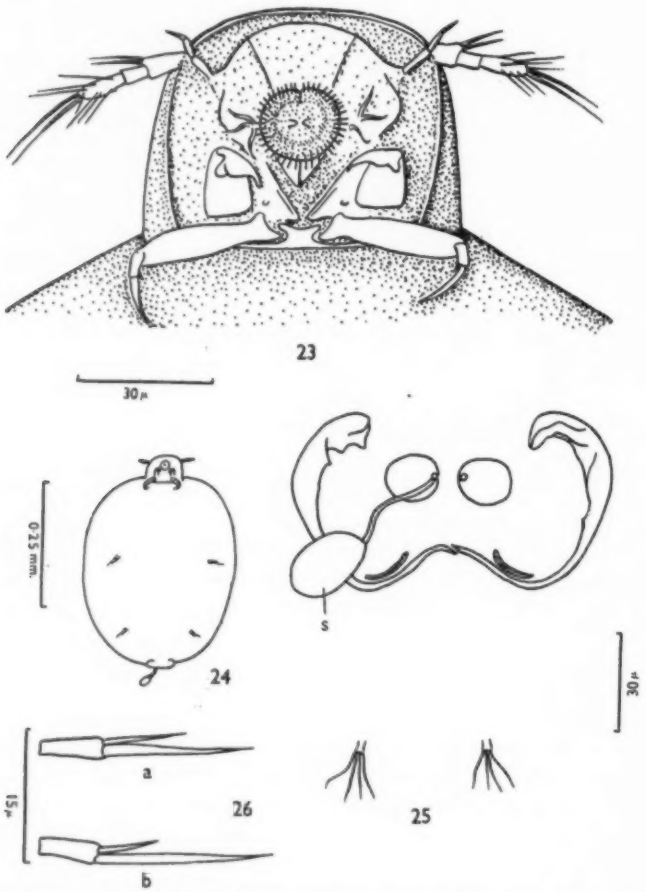
Sphaeronella valida Scott, 1905

Syn. *Sphaeronella minuta* var. *valida* Scott, 1905.

Material examined. One female from the brood pouch of *Megamphopus cornutus* Norman, taken off the Norfolk coast (53° 04 N, 01° 00 E) 12 fthms., September 1957. Collected by Mr R. Hamond.

The specimen from Norfolk is illustrated in Figs. 23–26. The total length of the specimen is 0·45 mm. The most important characters to be noticed are as follows. The head is naked, without any fringing hairs. The antennules are large, with three podomeres bearing a total of eleven setae, two of which are on the proximal podomere and nine on the distal podomere. The antennae

are distinct, with three podomeres. The maxillules have three processes, one of which is directed posteriorly. The maxillae have a large basal podomere which appears to be smooth and lacks the projections which are often found in other species of the genus. The maxillipedes are of the usual pattern, but are smooth, lacking setae. The ventral head skeleton is well developed,



Figs. 23–26.—*Sphaeronella valida*. 23, head of female, ventral view. 24, female, ventral view. 25, genital area and caudal rami of female ; s–spermatophore attached to entrance of spermatheca. 26, trunk limbs of female ; a–first, b–second.

and a bar, which bears a thickening in the middle, separates the head from the trunk. The trunk lacks hairs, and its limbs are placed more posteriorly than in most species of the genus. The genital area is surrounded by an incomplete ring of chitin, with a concave posterior border (Fig. 25). The caudal rami are placed well behind the genital area ; each ramus is slightly longer than wide and bears four setae.

Scott's drawings and description of *Sphaeronella minuta* var *valida* are inadequate to distinguish it from many other species in the genus. He gives no information about the antennae, maxillules, trunk limbs or the genital area, all of which must be examined before a species can be properly diagnosed.

The description given above of the Norfolk specimen should be regarded as a redescription, and the specimen regarded as a neotype—at least until such time as Scott's original specimen is located and redescribed. The status of *valida* has been raised to specific rank because Scott's drawings raise considerable doubts about *valida* being a mere variety of *minuta*.

The Norfolk specimen has been assigned to *valida* because the body shape is similar, and the caudal rami are located some distance behind the genital area (this is shown in side view in Scott's fig. 18). Further Scott's drawing of the maxillipede does not show any setae, which agrees with the description given above. Finally, the specimen was taken on the same host (Scott gives the host as *Melamphopus cornutus* Norman).

Distribution. Scotland, Firth of Forth (Scott); now recorded from Norfolk.

Host. *Megamphopus cornutus* Norman (Scott and present paper).

ACKNOWLEDGMENTS

I am most grateful to Dr J. P. Harding for his suggestion that I should examine this material, and for his helpful criticism of the manuscript.

SUMMARY

Rhizorhina ampeliscae Hansen is recorded from Guernsey and the Clyde area.

Five species of the genus *Sphaeronella* are recorded from British waters for the first time. One of these, *S. pikei*, is a new species.

Sphaeronella elegantula Hansen is shown to be a synonym of *S. leuckarti* Salensky.

The larva of *S. danica* and the male of *S. longipes* are described for the first time.

The following new hosts are recorded. *Aora typica* parasitized by *S. leuckarti*. *Erichthonius brasiliensis* parasitized by *S. danica*. *Ampelisca tenuicornis* parasitized by *S. frontalis*. *Pontocrates arenarius* parasitized by *S. pikei* sp. n.

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NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

15th April 1958

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.

President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MARCH 1958

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of March were 79 in number, including some domestic animals. The following are of special interest : two Kenya Blotched Genets, *Genetta tigrina erlangeri*, born in the Menagerie ; a Malay Tree Shrew, *Tupaia glis ferruginea*, born in the Menagerie ; a Squirrel Monkey, *Saimiri sciurea*, presented by Mrs G. E. Snow ; two Drills, *Mandrillus leucophaeus*, and a Crab-eating Raccoon, *Procyon cancrivorus*, received in exchange ; a Chinchilla, *Chinchilla laniger*, born in the Menagerie ; a Red-breasted Fruit Crow, *Pyroderus scutatus* (Shaw), new to the collection, presented by J. R. Newmark ; and two Golden-fronted Parrakeets, *Psiliopsiagon aurifrons aurifrons* (Lesson), new to the collection, received in exchange. During the same period there were 18 additions to the Menagerie at Whipsnade Park, apart from transfers from Regent's Park.

13th May 1958

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.

President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : APRIL 1958

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of April were 81 in number, including some domestic animals. The following are of special interest : three Pinche Marmosets, *Oedipomidas oedipus*, purchased ; a Clouded Leopard, *Neofelis nebulosa*, presented by Dr K. C. Searle, C.M.Z.S. ; a Humboldt's Woolly Monkey, *Lagothrix humboldti*,

presented by Mrs G. M. Rex ; two Ethiopian Yellow-billed Waxbills, *Coccopygia melanotis quartinia* (Bonaparte), new to the collection, presented by J. R. Newmark ; and a Banded Rock Python, *Liasis childreni* Gray, new to the collection, purchased. During the same period there were 27 additions to the Menagerie at Whipsnade Park, apart from one transfer from Regent's Park.

10th June 1958

Dr F. C. Fraser, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MAY 1958

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of May were 92 in number, including some domestic animals. The following are of special interest : a Humboldt's Woolly Monkey, *Lagothrix humboldti*, presented by Mr F. M. Davey ; a Greater White-crested Cockatoo, *Kakatoe alba*, presented by Miss Doris B. Carsons ; four Black-footed Penguins, *Spheniscus demersus*, presented by Mr Ronald J. E. Horsham ; two Bar-headed Geese, *Anser indicus*, received in exchange ; and a Copperhead, *Agkistrodon mokasen*, and a Western Diamond-backed Rattlesnake, *Crotalus atrox*, presented by the Central Texas Zoological Society. During the same period there were 26 additions to the Menagerie at Whipsnade Park.

THE CORRECT SCIENTIFIC NAME OF THE WEEPER CAPUCHIN

By W. C. Osman Hill

Of the numerous species or varieties of *Cebus* monkeys that have been described since the days of Linnaeus and Buffon, it is a matter of some doubt to which the term " weeper " should apply, especially in view of the embroiled state of the scientific nomenclature. In no mammalian genus has the taxonomy been so confused and the position today is very little better than in the days of F. Cuvier (1820) and Gray (1865, 1870) who both commented on the difficulties they encountered in dealing with the genus.

For the greater part of the 19th century and the first half of the present century the Weeper was generally known as *C. capucinus* auct. or as *Cebus apella*, a name which, however, has been conclusively shown to belong to quite another species—the Common Brown Capuchin previously known as *C. fatuellus* Linn. (*fide* Cabrera, 1917).

Setting aside all the so-called " tufted " capuchins as races of a single species *C. apella*, we are left, according to Lima (1945) and Hershkovitz (1949) with a series of " untufted " kinds which fall into three more or less distinct

groups. Of these the generally black-and-white Central American form (with races extending into Colombia) formerly known as *C. hypoleucus*, but now listed as *C. capucinus* Linn. is easily distinguished on pelage characters. Secondly we have the variants of *C. albifrons* Humboldt, widely ranging over northern South America, including the Amazonian region. By a process of elimination, therefore, there remains the Cai or Weeper, which has been known, as already noted as *C. capucinus* auct. until Cabrera (*loc. cit.*) extricated this name from its confuson and established the pertinency of *C. nigrivittatus* Wagner 1848. Lima and Hershkovitz both accepted this argument, but Husson (1957), though agreeing entirely with Hershkovitz's conception of the classification of the species and subspecies concerned, has recently shown that Wagner's name is untenable insofar as the name *nigrivittatus* was also used by Wagner for another monkey of a related genus (*Chrysothrix*=*Saimiri*). This would not in itself invalidate its use for a *Cebus* except for von Pusch's (1941) action, in his revision of *Cebus*, of uniting *Saimiri* therewith, thereby rendering the name homonymous. Husson gives quite a long and convincing argument for the total suppression of *nigrivittatus* (despite the subsequent quashing of von Pusch's arrangement) and recommends its replacement by the next oldest synonym, i.e. *C. olivaceus* Schomburgk (1848)—based, however, upon a supposedly different race of the same species.

Husson did not unfortunately concern himself with the nominate subspecies of the erstwhile *nigrivittatus* for the material he had under consideration all pertained to the race *olivaceus*.

In casting around for a name to apply to the erstwhile *C. n. nigrivittatus*, i.e. the typical Weeper, the only alternative seemed at first to resuscitate von Pusch's *leporinus*—a name specifically proposed to replace *nigrivittatus* on the rejection of the junior of Wagner's two specific names.

Nevertheless a systematic review of the possible synonyms of *nigrivittatus* inevitably leads to the name *griseus*. This is given by Hershkovitz as of Desmarest, 1820, with the comment that it is based primarily on the *sajou gris* of Buffon and Daubenton (1767) and is an absolute synonym of *barbatus* Humboldt which is a tufted *Cebus* and therefore equal to *C. apella*. Whether or no this be true of Desmarest's *griseus*, it certainly does not apply to F. Cuvier's *griseus*. Hershkovitz himself synonymizes this (p. 348) with *nigrivittatus* and admits that Cuvier's publication though dated 1824 in fact appeared as livraison 12 of his complete work in November 1819, thus antedating Desmarest anyway.

Now Cuvier's excellent plate of his *sajou mâle*, *C. griseus*, leaves no manner of doubt as to its representing a typical weeper, i.e. a monkey relegated by Lima and Hershkovitz to *nigrivittatus*. It clearly presents all the specific characters attributed to *nigrivittatus* by Lima and Hershkovitz, especially as to the shape of the black area on the vertex. Unfortunately no type locality is given, so that from this point of view it is uncertain to which of the five races recognized by Hershkovitz it strictly corresponds. Clearly the whole Formenkreis needs further revision, but whatever the outcome, it is clear that the specific name should be *griseus* F. Cuvier.

Most likely Cuvier's example—presumably a living specimen in the Paris menagerie—came from Guiana, most probably French Guiana. The type locality of *nigrivittatus* is on the Upper Rio Branco, i.e. in Brazilian Guiana. Hershkovitz, however, mentions one specimen (U.S.N.M. No. 261319) from the Paria Peninsula, Venezuela, as distinctly pale resembling closely the figure of the *sajou mâle* in Cuvier's plate. Yet he attributes this provisionally to a subspecies *brunneus* Allen, 1914 evidently on purely geographical grounds. With the wide range of individual age and sexual variation known to occur among this group of capuchins, it seems premature at this stage, pending further revision, to recognize so many races as Hershkovitz provisionally accepts. Apart possibly from *olivaceus* the rest (i.e. *brunneus* Allen ; *apiculatus* Elliot ; *castaneus* I. Geoffroy) may well provisionally be relegated to typical *griseus*.

Accordingly it is hereby advocated that the scientific name of the Weeper Capuchin should correctly be *Cebus griseus* F. Cuvier 1824 (1819) with Cuvier's plate representing the type and type locality restricted to French Guiana.

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PÈRE DAVID'S DEER, 1957

By E. H. Tong

At December 1957, the World Herd of Père David's Deer numbered 443. This increase of 63 over last year's figure (Proc. zool. Soc. Lond. vol. 129, p. 347) is very promising, and it is encouraging to note that this species of deer is becoming firmly established in many parts of the world.

During 1957, a pair of Père David's Deer was sent to Paris, and these are the first of this species to be exhibited in France for many years.

One of the females sent to Pekin in 1955 gave birth to a male calf in September 1957. This calf is the first to be born in China for almost a century.

	Herd 1956	No. Born	Deaths	Transferred to	Transferred from	Herd 1957
Antwerp, Royal Zoological Society of	2	—	—		1 Copenhagen Zoological Park	3
Basel, Zoological Garden	3	2	—			5
Berlin (East) Zoological Garden	3	2	—			5
Berlin (West) Zoological Garden	2	—	—			2
Chicago Zoological Garden	10	3	1			12
Cleveland Zoological Park	2	1	—			3
Cologne Zoological Garden	2	—	2			—
Copenhagen Zoological Park	5	4	—	1 Antwerp, Royal Zoological Society of		8
Edinburgh Zoological Park	5	—	—			5
Johannesburgh Zoological Garden	2	1	1			2
Lindermann, Mr R. New York	1	—	—			1
Milan, Dr Paladini	2	—	—			2
New York Zoological Society	8	—	—			8
Paris Zoological Park		—	—		2 Whipsnade Park	2
Pekin Zoological Garden	4	1	—			5
Prague Zoological Garden	3	—	—			3
Pretoria, National Zoological Gardens	3	1	1			3
Regent's Park	1	—	—			1
Riverdale Zoo, Toronto	5	1	—			6
Rotterdam Zoological Garden	2	—	—			2
Taronga Zoological Gardens, Sydney	14	—	—			14
Tollemache, Baron of, Suffolk	—	—	—		1 Woburn Park	1
Washington, Nat. Zoological Park	2	—	—			2
Whipsnade Park	21	4	2	2 Paris Zoological Park	2 Woburn Park	23
Woburn Park	278	112	63	2 Whipsnade Park 1 Tollemache, Baron of		324
						443

NOTES ON BRITISH MAMMALS

From

The Scientific Secretaries, Mammal Society of the British Isles

[Accepted 15th April 1958]

SOME OBSERVATIONS ON HARVEST MICE FROM THE CORN RICKS OF A HAMPSHIRE FARM

Introduction

An increase in the numbers of harvest mice (*Micromys minutus*) in corn ricks in the Oxford region has been reported by Southwick (1956). In 1942 and 1943 only four harvest mice were found in several hundred ricks in this locality compared with over 200 recovered from sixty-five ricks erected in 1954. The increase was believed to have occurred in the last year or two.

The present article concerns the occurrence of harvest mice found at threshing in a number of corn ricks on a farm at Popham, Hampshire, during 1955–57. The ricks were carefully proofed at the beginning of the operations and it is believed that all the harvest mice present were captured.

Numbers

In June 1955, four harvest mice were present in three ricks and in April 1956 twenty in three ricks. In 1957 harvest mice were frequently seen on the outside of nine ricks during the day, and in January eighteen were caught by hand or in live traps. These were sexed and weighed. During the threshing of seven ricks in March a further 119 mice were obtained. These were sexed, weighed, measured and examined internally for breeding condition.

Sex ratio

Of the total of 137 animals captured in January and March 1957, eighty-two (59·9 per cent) were males (Table 1). The difference in the numbers of each sex caught is significant ($\chi^2=4{\cdot}93$; $p=\cdot02-\cdot95$). Southwick also caught more males (56·0 per cent) than females although he did not always obtain complete populations.

TABLE 1.

Sex ratio in relation to weight

Weight group (g.)	Females	Males	Males per cent
–4·9	5	8	61·5
5·0–5·9	25	30	54·5
6·0–6·9	14	29	67·5
7·0–7·9	8	14	63·6
8·0 +	3	1	25·0
Totals	55	82	

Measurements

The average weight of the males was 6·07 g. (range 4·2–8·2 g.) and of the females 6·05 g. (range 4·4–10·2 g.). A female weighing 10·2 g. appears to be the heaviest recorded in this country.

Measurements of body length (tip of nose to anus) and tail length (anus to tip of tail) (Table 2) showed that in all but four animals the body was slightly longer (not more than 8 mm.) than the tail. The average body and tail length of males was 57·0 mm. (range 50–63 mm.) and 53·1 mm. (range 46–62 mm.) respectively and of females 57·1 mm. (range 50–69 mm.) and 53·3 mm. (range 48–66 mm.).

TABLE 2.

Average body and tail lengths of harvest mice in relation to sex and weight

Weight group (g.)	Females				Males			
	Number	Mean weight (g.)	Body length (mm.)	Tail length (mm.)	Number	Mean weight (g.)	Body length (mm.)	Tail length (mm.)
–4·9	5	4·7	52·0	49·0	8	4·7	54·8	50·0
5·0–5·9	24	5·6	55·4	49·3	29	5·5	56·3	52·2
6·0–6·9	10	6·3	56·1	52·7	23	6·4	57·9	54·2
7·0–7·9	7	7·4	64·0	62·0	11	7·2	58·1	54·8
8·0 +	1	8·4	67·0	53·0	1	8·2	63·0	59·0

Reproduction

Laurie (1946) found for the house mouse (*Mus musculus*) that if tubules in the cauda epididymidis were visible to the naked eye they invariably contained sperms. The fecundity of nineteen male harvest mice was thus determined by examining the cauda epididymidis with a hand lens (twelve fecund, seven non-fecund) and confirmed by microscopic examination of a stained smear of the epididymis. Thereafter it was decided that naked eye examination was sufficient. On this criterion thirty-five of the seventy-two males (48·6 per cent) were fecund. Fecundity appeared to be related to body weight (and presumably to age) as only 33·3 per cent of males of 5·0 g. or less were fecund compared with 63·9 per cent of those of greater weight. It was, however, more closely related to testis length ; only two out of thirty-four (5·9 per cent) with testes 3 – 4½ mm. in length being fecund compared with thirty-three out of thirty-eight (86·8 per cent) having tests 5 – 6 mm. long.

External and internal examination of females showed that all had imperforate vaginae and inactive ovaries.

Discussion

Little information is available on the status and distribution of *M. minutus*. Barrett-Hamilton & Hinton (1910–21) refer to annual fluctuations in its numbers. An apparent decline in recent years has been attributed to the use of reaping machinery (Harrison Matthews, 1952). The increase in numbers

of the harvest mouse reported by Southwick in the Oxford area may be more widespread. The numbers captured at Popham over the three years show that the animal is not scarce there and that an increase may have occurred. The numbers of harvest mice found in ricks may be affected by the date threshing occurs for there is evidence to suggest that they leave the ricks in the spring. It is noticeable that most of the animals captured near Oxford were obtained in February and March. At Popham the last two ricks were threshed in May and although numerous nests were discovered, only one harvest mouse was found. Nevertheless Jenkins (1957) notes that in Hampshire in the winter of 1955–56 there were few harvest mice except in some 15-month-old ricks.

Although further observations are desirable, it seems that there is a general excess of male harvest mice in ricks during the winter months. This is in direct contrast to the house mouse populations of ricks which usually contain an excess of females (Laurie, 1946). The sex ratio of harvest mice may, however, change during the breeding season. This has been observed in laboratory rats by King & Stotsenburg (1915) who found that the proportion of males was lowest in the height of the breeding season and highest at the extreme end.

Weight and body measurements suggest that mice of different ages were present in the rick populations and Millais (Barrett-Hamilton & Hinton, 1910–21) states that " harvest mice breed several times during the season, among wild vegetation, amongst corn and amongst corn ricks ". The larger females may be those which have borne young, for Cole & Hart (1938) have shown that pregnancy stimulates skeletal and tissue growth in the rat.

Southwick concluded from external examination that animals of both sexes captured between December and May were in a non-breeding state. Internal examination of the harvest mice captured at Popham showed that although some males were fecund as early as March females were then in a non-breeding condition, supporting the view that reproduction is confined to the summer months.

Direct observation indicates that harvest mice live near the outside of ricks. Small nests made of shredded grass were found amongst the stalks of the outermost sheaves. Aggressive behaviour was observed when disturbed animals entered the nests occupied by others. In captivity harvest mice are known to eat a varied diet ; they favour insects and frequently drink water, both of which are found most often on the outside of a rick. Some predation on harvest mice by rodents or other animals may occur in ricks since the skin of a freshly killed animal was discovered near the entrance to a rat hole.

ACKNOWLEDGMENTS

Thanks are expressed for assistance to Mr D. C. Drummond, Mr R. Redfern, Mrs M. Rowe and Miss E. Taylor.

SUMMARY

1. The numbers of harvest mice obtained from the corn ricks of a Hampshire farm at threshing are reported for the years 1955–57.

2. In January and March 1957, 137 harvest mice were captured from seven ricks. Males (82) outnumbered females (55); their average weights are given.

3. The average body measurements of 119 captured in March are recorded. An internal examination of these animals showed that almost one half of the males were fecund whereas all of the females were in a non-breeding condition.

4. Some observations were noted of the behaviour of harvest mice in corn ricks.

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F. P. Rowe.

NOTES CONCERNING FIVE SPECIES OF MAMMALS IN THE WEST COUNTRY

The occurrences reported below result from my interest in Siphonaptera (fleas) and my consequent search for hosts. In this search I have enlisted the aid of my pupils and friends various of whom are responsible for four of the records.

NOCTULE (*Nyctalus noctula*)

This bat is recorded from several localities in Gloucestershire (Walling, 1956). On 28th May 1956 two of my pupils, J. Knott and C. Masson, found a colony using several holes in a small wood near Churchdown, Glos. Two of the holes appeared to be old woodpecker cuttings and one was a rot hole in the scar where a large branch had broken off. All were about 18 feet above the ground in ash trees. The two boys collected three females and one immature specimen but one of the females gave birth between the time of collecting and delivery to me on 29th May. The parent weighed 25·86 g. and the offspring, which was fully formed and active, weighed 5·44 g. which is 21·03 per cent of the parent weight, or 17·3 per cent of the final pregnancy weight. The other immature specimen, obviously a few days older, weighed 8·96 g. These births were exceptionally early for Great Britain, the usual dates for England being from the third week in June to the first week in July. This year Knott has found another roosting hole at Brockworth, Glos., about 1½ miles from his first find. From this hole I have taken males and from the droppings several specimens of a rare muscid fly, *Fannia vespertilionis* Ringdahl, which has only been recorded in Britain on two other occasions. As a result of this find I would

very much like to see fresh samples of Noctule droppings from roost-holes from any locality.

LEISLER'S BAT (*Nyctalus leisleri*)

The previous reports of this species in Gloucestershire are in Tomes (1874) (near Cirencester and " in the course of the river Avon, in the counties of Warwick, Worcester and Gloucester ") and Matthews & Mayes (1949) (Stoke Bishop). Tomes' reference is repeated in Barrett-Hamilton & Hinton (1910–21).

Another of my pupils, A. Jones, took a specimen in an out-building at his home in Gloucester on 28th March 1955. His grandfather had brought a large bat home a few days previously from No. 7 M.U., R.A.F., Quedgeley, Glos., a few miles south of Gloucester. This bat escaped from its cardboard box and I suspect that the two reports are of one individual. However, without proof of my suspicions, the locality of this specimen must be Gloucester City.

BECHSTEIN'S BAT (*Myotis bechsteini*)

This bat's centre of distribution in England has long been known as Hampshire and the Isle of Wight with outlying records at Henley-on-Thames and Battle, Sussex. In 1953 a specimen was recorded from near Ludlow (Blackmore, 1953). The photographs in " The Times " (28th September 1953) of this specimen enabled me to recognize one brought to me on 17th September 1954 by another two of my pupils, R. H. Cooper and A. C. Durrant, who had found it dying on a footpath on their way to school. The bat was already dead when brought to me but was still warm and from its fur I removed a single specimen of *Basilia nana* (Diptera : Nycteribiidae). This fly had only been known previously in England from the Ludlow bat. The Gloucester bat had flown into the bedroom of a Mrs Whittington at about 2 a.m., her husband had hit it with a magazine and thrown it out of the window.

The Gloucester bat was displayed in a collection of mammal skins put by the Crypt School, Gloucester, into the Schools' Exhibition of the British Association for the Advancement of Science at Bristol in September 1955, and this brought me into contact with Mr R. W. Sawyer who had another specimen found by R. J. Loftus in a garage, Compton Durville, nr. South Petherton, Somerset, on 30th October 1954 at 9.30 p.m.

So few of these bats have been taken in England that a comparison of the present specimens is of interest :—

	Gloucester specimen	Shropshire specimen	Somerset specimen
Sex	male	male	?*
Fore-arm	39 mm.	40·9 mm.	37·3 mm.
Ear (greatest length)	25 „	19·9 „	20·6 „
Tragus	11 „	10·0 „	8·5 „
Lower leg	21 „	21·15 „	19·3 „
Hind foot (excluding claws) ..	9·5 „	8·82 „	8·2 „
Longest digit	59·5 „	60·1 „	48·2 „
Wing-span	215 „	237 „	*

* Not determinable from the skin.

There is one other fairly recent record of Bechstein's Bat in the west of England, that of Gooch (1956), reporting an occurrence near Swanage in 1947.

DAUBENTON'S BAT (*Myotis daubentoni*)

This bat has now been found in Gloucestershire, in the caves at Cranham by D. A. Humphries, D. Protherough and R. D. Ransome on 10th February 1957 (Walling, 1957) and by A. Iles on 10th March 1957. The identification of the first specimen has been confirmed by Mr Michael Blackmore and I saw the second and removed from it *Nycteribia kolenatii* Theodor (Diptera : Nycteribiidae), this being the first collection of the fly in Gloucestershire.

YELLOW-NECKED FIELD MOUSE (*Apodemus flavicollis*)

On 6th June 1955 I trapped a male of this mouse in the boundary hedge of the Crypt School grounds, Podsmead, Gloucester. The fleas which I obtained from the body appear to be the first to be recorded in detail from this species (George, 1957). I now have records of fleas from yellow-necked mice in Herefordshire, Kent and Suffolk and these recordings will be summarized in the future. Mr H. M. Hallett of Lea Bailey, nr. Ross-on-Wye, tells me that he has *seen* this mouse in his loft feeding upon stored apples. The loft is about ten yards on the Gloucestershire side of the Glos./Herefordshire boundary. Mr J. E. Knight of Doughton Cottage, nr. Ross-on-Wye also finds this mouse in his house and outbuildings.

Specimens of the species I bring forward as new records are deposited in the Gloucester City Museum with the exception of Daubenton's Bat and the Compton Durville bat which is in the Bristol City Museum.

ACKNOWLEDGMENTS

I am extremely grateful to Mr Michael Blackmore for confirmation of my identifications and very considerable help with this article. To all my pupils and friends who have brought animals to me I extend my sincere gratitude. Mr Sawyer must be thanked for so generously giving his specimen of Bechstein's Bat to the City Museum, Bristol.

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R. S. George.

A NOTE ON THE PINE MARTEN (*Martes martes*) IN WORCESTERSHIRE

Sir Charles Hastings (1834) was the last naturalist to include the pine marten in a fauna list for Worcestershire. From published accounts, which will be referred to later in this note, it seems that the marten disappeared from the county before 1886. It now appears from information which has recently come to hand, that the species survived until well into the present century in the north of the county.

While conducting a survey of west midland mammals, I was informed by H. R. Munro, chief forester on the Lickey Hills 1931–53, that an old gamekeeper, George Wright of Rednal, had seen martens on the Wenham estate on the Lickeys (which lie four miles north of Bromsgrove) in the early years of the century. The following account is prepared from a recorded interview we had with George Wright.

Wright worked on the Wenham estate from about 1897 to 1920 as forester and gamekeeper. The estate at that time included land behind the Old Rose and Crown Inn, as it is now called (Ref. SO/995758), and two small meadows on the opposite side of the road that passes the inn. This land was planted by Wright and it was in the plantations, which still exist, that martens were observed.

During the period roughly 1897–1907 game was preserved in the young plantations, which were then very dense. In 1907 game preservation was discontinued and from that time no martens were seen. Wright suggests that their presence over the ten-year period was due to the attraction of abundant game. Besides flying game there were plenty of rabbits and, at least during the early part of the time, an abundance of red squirrels.

Wright at the time of the interview was 78 years of age, intelligent and remarkably well preserved physically. He killed martens from time to time throughout the ten-year period and hung them on gibbets together with weasels and stoats. Thus there seems no reason to doubt the reliability of the identification.

This report of the late occurrence of the marten will now be considered in the light of earlier accounts. After Hastings, already referred to, comes de Hamel (1886), who believed that the marten was already extinct in the west midlands. R. F. Tomes (1901) mentions the last record known to him as being one " more than half a century since at Falke Mill, near Evesham ". Forrest (1913) evidently considered the species was absent from the midland counties since he refers to them wandering from Wales into Shropshire.

The latest definite record, in what we may call the Lickey area, which a search of the literature has produced, is one by W. H. Bath who observed a marten at close quarters in Sutton Park in 1884. Bath refers to the marten as " this now somewhat rare animal ". Although Sutton Park is in Warwickshire it lies little more than 12 miles from the Lickeys, a distance well within the range of the marten—Pitt (1938) notes a night's travelling of 15 miles. Admittedly the city of Birmingham lay between but at that date the Worcestershire border approached within five miles of Sutton Park.

Although Wright's record is later by nearly 60 years than the one referred to by Tomes its reliability need not be doubted on that account. Tomes was primarily a bat specialist and admitted his lack of acquaintance with the northern part of the county where the Lickeys are situated. Thus there seem good reasons for accepting the record. Probably, if land owners and game keepers active at the beginning of the century were questioned, other late occurrences of the marten in suitable areas in the west midlands would be reported.

I have to thank H. R. Munro for introducing me to George Wright ; I have also been glad to draw upon F. Fincher's knowledge of Worcestershire records.

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T. J. Pickvance.

MOLE AND STOAT ON EILEAN MOLACH, LOCH BA, ARGYLL

On Monday 12th August 1957 I visited the islands of Loch Ba and spent nearly three hours on Eilean Molach. At two places on that island, which is about fifty yards long, twenty broad, and two hundred from the shore, I found evidence of the presence of a mole (*Talpa europaea*). At one of these, seven hills of freshly excavated sandy and peaty soil were connected by a tunnel system. The tunnels were about two inches in diameter, and no more than three inches below the surface of the soil. At the other locality, around a mature rowan, there were four hills but the tunnels were less well defined. Later while rowing round Eilean Molach, I watched a stoat (*Mustela erminea*) moving along the shore rocks. The animal remained still for periods of up to ten seconds on top of them, and I had it in view with binoculars at a range of twenty yards for about a minute.

An intensive search was made on Eilean Molach for earthworms. None was found. Later I went ashore on the most easterly islet of Loch Ba, and on searching the jetsam on the shore, consisting of rotting vegetable matter, found an abundance of earthworms. No sign of any small mammal was seen on this islet. Returning to Eilean Molach I searched the jetsam there, but again failed to uncover an earthworm. The soil fauna of this island is, however, fairly rich in dipterous larvae, beetles, ants and spiders, and this community is probably dense enough to support small carnivorous mammals such as moles.

Except for the mole hills, no sign was seen of small mammals which might provide a food supply for the stoat, but the island is frequented by red grouse (*Lagopus scoticus*), and odd birds may possibly be taken. A pair were flushed, and droppings were found throughout the island, but I saw no trace of any kill.

The stoat, like the pine-marten (*Martes martes*) at Coille na Glas-leitire, Wester Ross, no doubt feeds to a great extent on blaeberry (*Vaccinium myrtillus*), as well as on insects, small mammals and birds.

The stoat would have had no difficulty in swimming across to the island ; the presence of the mole is more of a mystery. Mr Stewart, stalker in the Blackmount Estate has no record of moles having been introduced by man to Eilean Molach. The animal is common in arable and woodland soils at Loch Tulla, Glen Etive, and Glen Coe, but is probably very scarce on the Moor of Rannoch.

The distribution of the mole in the Scottish West Highlands is interesting. A similar case to the occurrence of the animal on Eilean Molach is reported by Dr D. N. McVean, who found mole hills on Eilean Mor and the smaller islet to the east of it, in Loch Sionascaig, Wester Ross. Mr J. Polson tells me that he has found mole hills on a grassy slope about 1,500 feet above sea-level on Ben a Vuinie, Kinlochewe, Wester Ross. I have found it widespread throughout mainland Argyll and West Inverness, with colonies in such isolated places as the Glomach gorge, Wester Ross, and the derelict in-bye ground at Skiary, inner Loch Hourn, Inverness-shire.

I should like to take the opportunity of thanking the proprietor of the Blackmount Estate for permission (through the Overseer, Mr J. Menzies) to visit the islands in Loch Ba, and for the provision of a boat.

J. Morton Boyd.

A FURTHER NOTE ON THE INCREASE OF HARES (*Lepus europaeus*) IN FRANCE

Recently I have had occasion to discuss the hare/rabbit ratio with several owners of shooting properties in France. The opinion is that although the rabbit is beginning to come back in modest numbers (but not everywhere) hares continue to increase. The following notes and figures were kindly supplied by Comte de Ganay, Monsieur Pierre Wertheimer, Monsieur Calmann-Levy and Madame Jean Couturié.

Year	Courances			La Presle	
	Rabbits killed	Hares killed	Method	Rabbits killed	Hares killed
1948	1,115	75	All shot	Not recorded	Not recorded
1949	2,333	180	,, ,,	15,847	102
1950	1,941	259	,, ,,	11,188	244
1951	700	26	,, ,,	9,096	131
1952	2,000	241	,, ,,	13,410	177
1953*	1	270	,, ,,	0	108
1954	18	226	84 netted	222	231
1955	29	369	285 ,,	97	511
1956	100	457	451 ,,	45	467 (up to Oct. only)

* Advent of myxomatosis.

(1) Shoot of approximately 4000 acres at Courances par Milly (Seine et Oise) lying to the west of the Forest of Fontainbleau, an area in which foxes are protected. Half the land is arable and the other half very poor forest which is wired in. A series of trap doors in this wire fencing is closed while the "fur" is feeding at night and the animals shot or netted in the arable area the following day. Rabbits are shot once a week from September to March and three organised hare shoots take place during the year.

The detailed figures for the last ten seasons can be compared with those supplied by Monsieur Pierre Wertheimer for his 4000 acre shoot at La Presle, Cerdon-du-Loiret (see also Proc. zool. Soc. Lond. **127** (1956), p. 445.

(2) Shoot of approximately 2500 acres at Marcilly en Gault (Loir et Cher). The mean number of rabbits shot in this area before the advent of myxomatosis was 10,000 and 30 hares per year. In 1927 the hares succumbed to a disease diagnosed by the owner as tularaemia and were practically exterminated. Their numbers increased to what was considered the normal population, i.e. an estimated total of about 60 on the property, during the next three years. Directly after the destruction of the rabbit by myxomatosis the hares began to increase. During 1956–57 320 hares were shot and the estimated number present is now 1000.

(3) A small shoot of approximately 1000 acres on sandy soil at Chateau de Mesnil, Savigné-Evéque, Sarthe. The annual bag of rabbits before myxomatosis was 3000 per annum and the number of hares "under ten". Since the destruction of the rabbit the annual kill of hares has risen to 100. These figures are very similar to those recorded at Ashton, Peterborough (Rothschild and Marsh, 1956).

Comte de Ganay and Baron Eli de Rothschild expressed the view that the netting instead of shooting of hares could account for the increase on their estates, since they considered that previously a fair number were "peppered" during shoots, and as a direct consequence failed to breed. Comte de Ganay considered that foxes on his property were reduced by 50 per cent since the advent of myxomatosis. Other owners offered no explanation, but there was unanimous agreement that since the disappearance of the rabbit, hares had increased in France.

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Miriam Rothschild.

WINTER ROOSTS OF BATS IN WEST SUFFOLK

Around Bury St. Edmunds there are a number of man-made caves dug from the chalk which are used as winter roosts by bats. These caves have been described by Francis (1952). The series of caves where observations have been made, Horringer and the Glen, are about two miles (3·2 km.) apart.

The Horringer series is the larger consisting of about 530 yards (484 metres) of caverns, whereas the Glen series comprises about 200 yards (183 metres). Observations have been made on the bats since 1947 and bats have been ringed since 1949. Initially aluminium rings bearing the address " Saffron Walden Museum " were used (through the kindness of Mr K. Burtsal), and later similar rings stamped " ZOO UCNW BANGOR ". Currently we are using rings obtained through the Mammal Society of the British Isles, and those bats which we have ringed previously with other rings are re-ringed as they come to hand.

Four species of bat have been found regularly in the caves (see also Gilbert, 1948), *Myotis nattereri*, *M. daubentoni*, *M. mystacinus* and *Plecotus auritus*. Between autumn 1949 and spring 1957 we have handled at Horringer 151 *M. daubentoni*, 119 *M. nattereri*, 60 *M. mystacinus*, 23 *P. auritus*, all of which were ringed. Representatives of each species have been found during all winters in which observations were made. In addition during the winters 1955–56 and 1956–57 a total of four *Barbastella barbastellus* were found.

Between autumn 1951 and spring 1957 the following bats were ringed at Horringer : *M. daubentoni* 53 males 47 females, *M. mystacinus*, 24 males 18 females, *M. nattereri* 50 males 33 females, *P. auritus* 5 males 7 females, *B. barbastellus* 4 males. The preponderance of males in the first three species is not significant at the 5 per cent probability level and the absence of female *B. barbastellus* barely so. The grand total of all bats ringed at Horringer (138 males 103 females) shows a preponderance of males which is significantly different from a 1 : 1 sex ratio at the 2·5 per cent probability level ($\chi^2=5{\cdot}08$). Of the bats ringed only one has been returned to us from outside the caves ; this was a female *P. auritus* ringed at Horringer on 9th April 1957 and found dead on 8th October 1957 about $1\frac{5}{8}$ miles (2·6 km.) away.

Table 1 shows the winter-by-winter recapture data for the three species of *Myotis*. These data suggest that *M. daubentoni* shows more preference for the continued use, year after year, of the same winter roost than do the other two species. An alternative hypothesis is that *M. nattereri* and *M. mystacinus* return to a winter roost as regularly as *M. daubentoni*, but stay in any roost for a shorter time ; the data (Tables 2 and 3) are not sufficient to substantiate this. The habit shown by *Myotis* spp. of hiding in crevices, and thus escaping detection, is a complicating factor.

During the summer months the bats are virtually absent from the caves, recolonisation taking place during late September and October. During the following April the caves become empty once more. The extent of the summer dispersal of bats from the caves is unknown. The neighbourhood of Bury St. Edmunds abounds in bats during the summer but there is no reason to doubt that at least a few bats found in West Suffolk may fly considerable distances from their winter roosts, as has been demonstrated on the Continent (Eisentraut, 1935 ; Bels, 1952, van Heerdt & Sluiter, 1957). Several *B. barbastellus* were noted in flight about three-quarters of a mile (1·2 km.) from the Horringer caves in September 1950. Bats believed to be *M. daubentoni* have been seen frequently along the nearby valley of the River Lark. In addition to these *P. auritus* is abundant in West Suffolk. Although we have no first-hand evidence

that *M. mystacinus* and *M. nattereri* are summer residents in West Suffolk it seems unlikely that the whole winter population emigrates during the summer. *M. mystacinus* is regarded as extremely rare in East Anglia (Sergeant & Harrison, 1947 ; Beirne, 1948).

TABLE 1

Total ringings and recaptures during successive winters.

			M. daubentoni			
1949–50	**44**					
1950–51					Total ringed 151	
1951–52	1	**22**				
1952–53						
1953–54	1	0	**17**			
1954–55	4	3	4	**20**		
1955–56	3	2	0	1	**6**	
1956–57	4	2	4	1	1	**42**
			M. nattereri			
1949–50	**33**					
1950–51					Total ringed 119	
1951–52	0	**28**				
1952–53						
1953–54	0	0	**3**			
1954–55	1	0	0	**13**		
1955–56	0	0	0	0	**8**	
1956–57	0	0	0	1	8	**34**
			M. mystacinus			
1949–50	**14**					
1950–51					Total ringed 60	
1951–52	0	**9**				
1952–53						
1953–54	0	0	**4**			
1954–55	1	0	0	**10**		
1955–56	1	0	0	1	**18**	
1956–57	1	1	0	0	0	**5**

The initial captures are in heavy type with the subsequent captures beneath.

Although some bats using the caves are torpid, some even bedewed, many are active during the winter months, as has been found also in horse-shoe bats (e.g. Hesketh, 1951 ; Hooper & Hooper, 1956). On 30th December 1947 several pairs of *Myotis* were seen *in coitu*. The female of one pair was taken and proved to be *M. nattereri*. Bats performing their toilet have been seen on several occasions. An indication of the extent of winter activity is given in Table 2 which shows that the population at Horringer is constantly changing. Many bats which are not found on the sampling date immediately after their handling are found on a subsequent occasion during the same winter (Table 2). Unfortunately it is impossible to gauge from these data the extent to which the change in population is normal and not a reaction to handling. Observations made at the Glen during the winter 1956–57 provide *a priori* evidence that handling reduces the numbers found in the caves (Table 3). It is possible that handling makes the bats more furtive, and therefore more difficult to find, rather than more active. On 29th December 1956 the Glen was visited after a lapse of almost six years and the bats present ringed. Immediately after this

TABLE 2

Captures of bats in Horringer caves during the winter 1956–57

		M. daubentoni		*M. mystacinus*		*M. nattereri*		*P. auritus*		*B. barbastellus*		Total
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
20/10/56	A	3	11	1	1	1	0	0	0	0	0	17
	B	1	1	0	0	0	–	–	–	–	–	2
	C	1	1	0	1	0	–	–	–	–	–	3
10/11/56	A	11	9	1	1	0	0	0	0	0	0	22
	B	0	1	0	0	–	–	–	–	–	–	1
	C	2	1	0	0	–	–	–	–	–	–	3
15/12/56	A	7	4	1	2	11	3	2	0	0	0	30
	B	0	3	0	0	1	1	1	–	–	–	6
	C	1	1	1	1	4	2	0	–	–	–	10
31/12/56	A	3	6	0	0	12	5	2	0	2	0	30
	B	1	0	–	–	0	0	0	–	0	–	1
	C	0	1	–	–	0	0	0	–	0	–	1
5/1/57	A	4	2	0	0	3	1	0	0	0	0	10
	B	2	0	–	–	0	0	–	–	–	–	2
	C	1	0	–	–	0	0	–	–	–	–	1
2/2/57	A	7	2	0	1	6	7	0	0	0	0	23
	B	0	0	–	0	0	0	–	–	–	–	0
	C	0	0	–	0	0	0	–	–	–	–	0
9/3/57	A	2	1	1	0	1	1	0	0	0	0	6
	B	0	0	0	–	0	0	–	–	–	–	0
9/4/57	A	0	0	1	0	0	0	0	1	0	0	2
22/7/57	A	0	0	0	0	0	0	0	0	0	0	0

A—captures on the date given.
B—captures on date A also captured on the next sampling date.
C—captures on date A but not on date B although captured subsequently during the winter.

there was a dramatic drop affecting all species. There is circumstantial evidence that ringing affected the numbers of bats found at any one time in the Horringer Caves. Table 4 lists the number of bats seen at Horringer on the visit nearest New Year's Day in a number of winters. During the winter 1948–49, before ringing began, 70 bats were counted. Ringing was begun in

TABLE 3

Captures of bats in the Glen caves during the winter 1956–57

		M. daubentoni		*M. mystacinus*		*M. nattereri*		*P. auritus*		Total
		♂	♀	♂	♀	♂	♀	♂	♀	
29/12/56	A	11	7	1	1	11	5	3	2	41
	B	1	0	1	0	1	0	1	0	4
5/1/57	A	4	1	1	0	3	2	2	0	13
	B	0	0	0	–	0	1	0	0	1
16/2/57	A	8	1	1	1	6	7	0	0	24
	B	0	0	1	0	0	0	–	–	1
23/3/57	A	0	1	1	0	0	1	0	0	3

A—captures on date given.
B—captures on date A also captured on the next sampling date.

autumn 1949 and thereafter the numbers have not exceeded 50 at any visit and are currently much lower. The figure for the winter of 1948–49 may have been unusually high as during the previous winter it was estimated that about forty bats were in the caves at Christmas.

TABLE 4

Number of bats found in the Horringer caves on the sampling date nearest January 1st in several winters

	M. daubentoni	*M. mystacinus*	*M. nattereri*	*P. auritus*	*B. barbastellus*	Total
28/12/49	17	5	19	0	0	41
27/12/51	12	5	14	0	0	31
28/12/54	4	4	2	0	0	10
31/12/56	9	0	17	2	2	30

The ringing data (Table 1) give information on longevity of some of the species although the data compare poorly with those of van Heerdt & Sluiter (1957). Two male *M. daubentoni* ringed on 30th November 1949 at Horringer were found there on 10th November and 31st December 1956 respectively, giving a minimum life-span of more than seven years. A female ringed on the same date was recaptured also at Horringer on 15th September 1955 giving a life-span of at least six years. Similarly a male *M. mystacinus* ringed at Horringer on 4th March 1950 was recaptured on 9th April 1957, a period of over seven years. One female *M. nattereri* was found during the winter of 1951–52 at Horringer and again during the winter 1956–57, the female being recaptured at the Glen. Another female *M. nattereri* crossed from the Glen to Horringer between 29th December 1956 and 2nd February 1957. These are the only recorded interchanges between the two cave series. Neither *P. auritus* nor *B. barbastellus* has been found in the caves in two successive years.

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O. Gilbert.
R. Stebbings.

NOTICE

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